

VEGETATION STUDIES IN THE HUMANSDORP REGION OF THE
FYNBOS BIOME

BY

RICHARD MARK COWLING

Submitted in part fulfilment of the
requirements for the degree

DOCTOR OF PHILOSOPHY

in the

Department of Botany

Faculty of Science

University of Cape Town

1982

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

This thesis is dedicated to the life works of the
late J.P.H. Acocks, and the
late M.R. Levyns

The question only is, where to draw the line?

S. Schonland (1919) commenting on biogeographic division
in the south eastern Cape.

The view is taken that the ecology of South Africa
is something dynamic

J.P.H. Acocks (1953)

It seems inescapable that both proximal and ultimate
ecological interpretation must be at the level of
individuals

J.L. Harper (1980)

ABSTRACT

This thesis comprises five papers dealing with syntaxonomy, history, species diversity and growth form distribution in Cape shrublands and non-Cape vegetation types (subtropical thicket, Afromontane forest) in the Humansdorp region of the Fynbos Biome.

The first paper is a re-evaluation of vegetation concepts in the study area and, more generally, in the Fynbos Biome and adjacent biomes. Syntaxa are characterized in terms of floristics (including biogeographical affinities and patterns of endemism), structure and dynamics. In the second paper both descriptive and historical approaches are used to generate hypotheses to explain vegetation history during the last glacial to Holocene sequence. The third paper investigates, and seeks explanations for, diversity relations in the vegetation types of the study area. Both historical and ecological factors are used to predict patterns of species diversity. In the fourth paper patterns in the relative importance of structural attributes and growth forms along fynbos and non-fynbos coenoclines are studied. An appendix paper focusses on the distribution of C_3 and C_4 grasses in the Cape shrublands of the study area.

It was concluded that descriptive studies such as this have much value in clarifying vegetation concepts and generating hypotheses to explain variations in community structure. However, as management and conservation are the

major aims of the Fynbos Biome Project, future studies should concentrate on the reproductive biology and regeneration niches of plants in the fire-prone Cape shrublands. From the results of such studies a predictive knowledge of Cape shrubland dynamics will emerge - the key to judicious management.

PREFACE

For many years I have been fascinated by the vegetation and scenery of the south eastern Cape, and in particular, the Humansdorp region. When passing through or working in the area I was always amazed and intrigued by the enormous changes in vegetation structure and composition over seemingly trivial distances or environmental gradients. Here subtropical thicket is found in a matrix of temperate Cape fynbos; Afromontane forests grow in the cool wet mountains while dry karroid scrub thrives a few hundred meters below in the valley bottoms. Amidst this biogeographical complexity are even more complex and interesting dynamic interactions. In many sites perturbations result in a series of cover states each dominated by species characteristic of different phytochoria. Mismanagement of subtropical and temperate grasslands results in their replacement by karroid and Cape shrublands respectively. The S.E. Cape accepts, it would appear only too willingly, the weeds of all the phytochoria which converge there. I have seen near Port Elizabeth a mixed stand of Acacia karroo, Chrysocoma tenuifolia, Elytropappus rhinocerotis and Leucadendron salignum invading a disturbed grassland.

The S.E. Cape is truly a region of contrast. Along with this complexity goes the challenge of unsolved problems. Vegetation characterization in the S.E. Cape is not an easy task: it provides the challenge of comparative studies in chorologically disparate and dynamically complex communities. It is precisely these challenges which inspired this study.

Many individuals have influenced profoundly my understanding of S.E. Cape vegetation. Winston Trollope of the University of Fort Hare, sharpened my appreciation of agro-ecological problems, particularly in the rural "homelands". Mr. C.J. Skead of Grahamstown, a naturalist with an astonishing depth of knowledge, brought to my attention the more subtle interactions between plants and animals - an approach that went beyond the grass-ungulate relationship. No single worker in the area has had a greater influence on my thinking than the late J.P.H. Acocks. His brilliant overview of vegetation patterns, dynamics and history, articulated in a slim volume entitled "Veld types of South Africa", forms the basis of this study, the groundwork of assertions to test, reject and refine.

This study would not have been possible without the enthusiastic support of Mr. Brian Huntley of the CSIR. I thank him for his encouragement and trust that this work is sufficient reward for his persistent efforts on my behalf. I am deeply indebted to my supervisor, Prof. Eugene Moll of the University of Cape Town, who set me free to slip into the paradigms of my choice, but who always retained a willingness to help and a friendly enthusiasm.

A great number of colleagues have enriched my experience during the course of this study. Ken Tinley increased greatly my understanding of geo-ecological processes and soil-moisture relationships. He taught me to see the structure and dynamics of certain vegetation types in the study area in their tropical African context. Bruce Campbell and I had many valuable discussions on the structure, diversity, dynamics and history of fynbos and related shrublands. Bruce gave selflessly of his time to help me with the arduous task of manipulating large data sets for computer analyses. Shirley Pierce was always prepared to criticize often sloppy manuscripts and we had many useful discussions which helped to sharpen vague notions into testable theories, and improve expression. Peter Linder introduced me to many important biogeographical concepts. During our frequent field trips in the S.E. Cape I benefitted greatly from discussions and arguments arising from the interaction of his systematic-evolutionary approach and my ecological-evolutionary approach. I thank also William Bond, Charlie Boucher, Johan Breytenbach, Lucia Jamison, Fred Kruger, Jeremy Midgley, Toni Milewski, Karl Schütte, Ray Specht, Hugh Taylor, Walt Westman and the late Prof. Bob Whittaker for valuable discussion and help at various stages during the course of this study. Many of the abovementioned are fellow participants of the Fynbos Biome Project. The generous communication of ideas will undoubtedly contribute to the overall success of the project.

Assistance given by officials of the Department of Agriculture and Fisheries is gratefully acknowledged. Henry Smith of the Humansdorp extension office acted as liaison between me and the Humansdorp farming community and helped with the initial selection of study sites. Estelle Brink and Miss L. Britten of the Botanical Research Unit at the Albany Museum readily gave up their time to help with the identification of plant specimens.

I thank Mrs. Rose Elliot for typing preliminary drafts of some papers and for photocopying services. A special word of thanks to Mr. and Mrs. S. Jarman for typing and checking the entire manuscript.

This study forms part of the Fynbos Biome Project and was funded by the CSIR. I thank Ms. Margie Jarman of CSP : CSIR for liaison and other supporting facilities.

TABLE OF CONTENTS

	Page
PREFACE	
GENERAL INTRODUCTION	1
PAPER 1: A syntaxonomic and synecological study in the Humansdorp region of the Fynbos Biome	6
PAPER 2: Phytochorology and vegetation history in the S.E. Cape, South Africa	128
PAPER 3: Diversity relations in Cape shrublands and other vegetation in the S.E. Cape, South Africa	205
PAPER 4: A comparison of fynbos and non-fynbos coenoclines in the lower Gamtoos River Valley, S.E. Cape, South Africa	253
GENERAL CONCLUSIONS	289
APPENDICES	
APPENDIX 1: The occurrence of C ₃ and C ₄ grasses in fynbos and allied shrublands in the S.E. Cape, South Africa	293
APPENDIX 2: Numerical methods of classification and gradient analysis: a brief overview	314
APPENDIX 3: Check list and geographical distribution of taxa	327
APPENDIX TABLES:	
1. Coastal dune communities, Humansdorp region	
2.1 Grassy Fynbos communities on Table Mountain sandstone, Humansdorp region	
2.2 Kaffrarian Thicket community on Table Mountain sandstone, Humansdorp region	
3.1 South Coast Renosterveld communities on Bokkeveld shale, Humansdorp region	
3.2 Subtropical Transitional Thicket communities on Bokkeveld shale, Humansdorp region	
4. Communities on Enon conglomerate, Humansdorp region	
5.1 Cape Fynbos and Coast Renosterveld communities of the lower Gamtoos River Valley	
5.2 Subtropical Transitional Thicket and Afromontane Forest communities of the lower Gamtoos River Valley	

ERRATA

Page numbers 125 and 158 omitted, and page number 218 duplicated.

GENERAL INTRODUCTION

The Fynbos Biome (*sensu* Kruger 1978) comprises much of the warm temperate, south western and southern portion of South Africa. Biome vegetation is characterized by fynbos, a broad category of shrublands which are included in a global heathland concept (Specht 1979). Acocks (1953) recognized three fynbos veld types - Fynbos (69)*, False Fynbos (70) and Coastal Fynbos (47). Biome types which are non-fynbos are the transitional shrublands, Strandveld (34a) and Coastal Renosterveld (47), which link the fynbos of the Cape phytochorion (*sensu* Werger 1978) to vegetation types of adjacent phytochoria. Despite the appearance in recent years of reviews on Cape fynbos and related shrublands (Taylor 1978; Kruger 1979; Boucher and Moll 1980), a precise characterization and delimitation of biome vegetation types was still lacking at the time when this study was initiated. Acocks (1953) in his outstanding study of South African veld types, skirts the problem of fynbos complexity. His breakdown of fynbos into three veld types (see above) is readily acknowledged as preliminary and simplistic. There is clearly scope for much more descriptive work on biome vegetation.

Since 1978, concomitant with the emergence of the Fynbos Biome Project, there has been an upsurge of research activity in the biome. As part of the initial baseline study phase of the project many workers have undertaken descriptive studies aimed at the classification and characterization of biome vegetation both on an intensive and extensive scale (Bond 1981; Boucher in prep; Campbell in prep; this study). These studies have been designed to realize "the overall and ultimate objective of the (Fynbos Biome) project to provide sound scientific knowledge of the structure and functioning of constituent ecosystems as a basis for the conservation and management of the Fynbos Biome." (Kruger 1978). Descriptive classificatory studies generate vegetation units which, despite the philosophical dialectics on the nature of vegetation, are essential for agricultural and conservation management. Descriptive studies are also an inventory of the composition and areal extent of communities at a given point in time and thus acquire historical import. This is especially true of the lowland ecosystems of the biome where the few relics of natural vegetation are fast disappearing.

* Refers to Acocks (1953) veld type number

The present study comprises a classification and characterization of communities and an investigation into the ecological and evolutionary factors which govern community distribution, structure, dynamics, history and species diversity. As such this study is the result of a largely inductive and descriptive approach which employed multivariate methods of classification and correlation as the principal analytical tools.

For many reasons I chose, as a study area, the eastern region of the Fynbos Biome. Firstly the region's vegetation and flora have sustained my interest for many years. I believe that a strong and consuming interest in a subject is conducive to an imaginative output. Secondly the eastern region of the biome forms part of the south eastern (S.E.) Cape, an area of remarkable vegetational complexity, which is a convergence zone of four African phytochoria (Werger 1978; Gibbs Russel and Robinson 1981). I felt that if I could develop sound syntaxonomic concepts in this complex region, these concepts could then be extrapolated readily to the less complex core regions of the biome. An exploration of the biogeographical complexity of the S.E. Cape and its implications for vegetation change is, in itself, a major focus of this study. Thirdly the S.E. Cape comprises a tension zone where a combination of a transitional and variable climate and species assemblages of diverse phytochorological affinities have resulted in communities highly vulnerable to the destabilizing influences of settled agriculture, resulting in the invasion and thickening-up of weedy species (Trollope 1980). If we are to manage vegetation for maximum sustainable livestock production on rangeland or for maximum diversity in conserved areas, a predictive knowledge of the dynamics of vegetation change in response to man-induced perturbations is essential. Thus one of the aims of this project was to study the dynamics of grazed and fire-prone shrublands. It was for this reason that I sampled sites which reflected the full range of disturbance regimes encountered in the study area. Although the normal practice in phytosociological surveys is to restrict sampling to relatively undisturbed mature vegetation, I felt that this approach has serious shortcomings in that it ignores the dynamic component of vegetation. I located my intensive study site in the Humansdorp region of the S.E. Cape. Within an area of approximately 300 km² I was able to study typical biome communities including three fynbos types and coast renosterveld as well as subtropical thicket and Afromontane forest, the two last mentioned being non-biome types which are patchily distributed in the biome mainly along the southern coastal forelands and mountains. The overall aims of the study were as follows:

- 1) Classification of vegetation into syntaxa and a characterization of syntaxonomic concepts in terms of floristics, structure, phytochorological affinities, patterns of endemism and dynamics.
- 2) The generation of hypotheses to explain the history of vegetation types in the study area and, as far as possible, to generalize these hypotheses for the S.E. Cape and the Fynbos Biome.
- 3) An investigation of the factors regulating the evolution and maintenance of species diversity in the major vegetation types.
- 4) A comparative study of the distribution and importance of growth forms and structural-functional attributes in fynbos and non-fynbos vegetation.

The results of the study are presented in four major research papers. Paper I deals with the first aim as outlined above. In this paper I present a syntaxonomic hierarchy of classes, orders and communities. The discussion is focussed on the level of the order which is roughly equivalent to an Acocks (1953) veld type. I regard the order concepts as a second approximation after Acocks' (1953) earlier work in the region. They are essentially working hypotheses, to be refined or rejected by later workers.

The second paper is an account of the phytochorological complexity and vegetation history of the study area. I employed a descriptive and historical approach to generate hypotheses to explain vegetation changes during a glacial-interglacial sequence. These hypotheses are based on rather flimsy historical evidence but have been generalized so that testable predictions can be readily deduced from them. In future years I hope that evolutionary taxonomists and palaeoecologists will collect the appropriate data to test these assertions.

The third paper is a comparative study of the factors regulating the evolution and maintenance of species diversity in fynbos and non-fynbos vegetation in the study area. Both historical and ecological factors were investigated for possible causal relationships with species diversity. The role of disturbance factors including fire, bush-cutting and grazing were explored to test non-equilibrium diversity models.

In the fourth and final paper I tested the hypothesis that relative importance of fynbos growth forms and structural-functional attributes could be explained in terms of low levels of available nutrients whereas the structure of non-fynbos communities could be interpreted largely in terms of variations in climate and soil moisture. From this hypothesis it can be deduced that along a gradient of increasing soil moisture, there would be less variation in

fynbos structure than non-fynbos structure, due to the overriding importance of low nutrients in determining the structure of the former type (cf. Specht 1979; Cowling and Campbell 1980). I tested this by comparing the structure of fynbos and non-fynbos coenoclines (cf. Whittaker 1967) along similar environmental gradients in the lower Gamtoos River Valley region of the study area.

The appendices include a short paper on the relative occurrence of C₃ and C₄ grasses in the fynbos and renosterveld communities of the study area, a brief resumé on methods of phytosociological data analysis, the phytosociological tables and a check list of the sample flora showing the classification of species into phytochorological groups.

An abstract precedes each of the research papers. These provide a concise summary of the results and principal conclusions of each paper and should enable readers to identify the basic content of the papers quickly and accurately.

References

- Acocks J P H 1953. Veld types of South Africa. Memoirs of the Botanical Survey of South Africa 28, 1 - 192.
- Bond W J 1981. Vegetation gradients in the southern Cape mountains. MSc Thesis, University of Cape Town.
- Boucher C and E J Moll 1980. South African mediterranean shrublands. Mediterranean-type shrublands. F di Castri, D W Goodall and R L Specht (eds). Elsevier, Amsterdam. pp 233 - 248.
- Cowling R M and B M Campbell 1980. Convergence in vegetation structure in the mediterranean communities of California, Chile and South Africa. Vegetatio 43, 191 - 197.
- Gibbs Russel G E and E R Robinson 1981. Phytogeography and speciation in the vegetation of the eastern Cape. Bothalia 13, 467 - 472.
- Kruger F J 1978. A description of the Fynbos Biome Project. South African National Scientific Programmes Report No. 28. CSIR, Pretoria.
- Kruger F J 1979. South African Heathlands. Heathlands and related shrublands of the world. A. Descriptive studies. R L Specht (ed). Elsevier, Amsterdam. pp 19 - 80.
- Specht R L 1979 (ed). Heathlands and related shrublands of the world. A. Descriptive studies. Elsevier, Amsterdam.
- Taylor H C 1978. Capensis. Biogeography and ecology of southern Africa. M J A Werger (ed). Junk, The Hague. pp 171 - 229.
- Trollope W S W 1980. Encroachment and control of indigenous undesirable plants in the eastern Cape. Agricultural Development Research Institute, University of Fort Hare.
- Werger M J A 1978. Biogeographical division of southern Africa. Biogeography and ecology of southern Africa. M J A Werger (ed). Junk, The Hague. pp 147 - 170.
- Whittaker R H 1967. Gradient analysis of vegetation. Biological Review, 42, 207 - 264.

PAPER 1

A SYNTAXONOMIC AND SYNECOLOGICAL STUDY IN THE HUMANSDORP
REGION OF THE FYNBOS BIOME

ABSTRACT

A hierarchical syntaxonomic scheme of vegetation in the eastern border of the Fynbos Biome (Humansdorp region) is presented as a second approximation after the earlier work by Acocks (1953) in the area. Details on the physiography, geology, climate, soils, historical features and present management of the area are given to provide the setting for this and other papers dealing with community characterization and ecological relationships, dynamics, structure and biogeography. A community classification was generated using a hierarchical numerical classificatory technique (TWINSpan) which produced ordered two-way phytosociological tables. Tabular comparisons and final sorting of tables is according to the methods of the Zurich-Montpellier School. Higher syntaxonomic ranks (classes and orders) are subjectively defined. Four classes, seven orders and 22 communities are recognised in the study area. The classes are Cape Fynbos Shrublands (3 orders, 10 communities), Cape Transitional Small-leaved Shrublands (1 order, 4 communities) Subtropical Transitional Thicket (2 orders, 6 communities) and Afromontane Forest (1 order, 2 communities). Discussion of the scheme is focussed on the level of the order (roughly equivalent to a veld type). In addition to diagnostic floristic elements, syntaxa are further characterised using biogeographic, structural and habitat criteria. The role of historical land use on vegetation dynamics and interrelationships is briefly discussed.

As far as possible syntaxonomic concepts are extrapolated to the entire Fynbos Biome as well as biomes adjacent to its eastern boundary. Certain syntaxa are examined relative to the shrubland/heathland concepts developed for mediterranean-type ecosystems.

CONTENTS

	Page
Introduction	9
1.0 Study Area	10
1.1 Physiography	12
1.2 Geology	13
1.3 Climate	17
1.4 Soils	24
1.5 Historical land use	31
2.0 Methods	34
2.1 Data collection	34
2.2 Data analysis	38
2.3 Community dynamics	41
3.0 The Syntaxa	45
3.1 Cape Fynbos Shrublands	45
3.1.1 South Eastern Mountain Fynbos	49
3.1.2 Grassy Fynbos	52
3.1.3 South Coast Dune Fynbos	60
3.2 Cape Transitional Small-leaved Shrublands	70
3.2.1 South Coast Renosterveld	74
3.3 Subtropical Transitional Thicket	83
3.3.1 Kaffrarian Thicket	89
3.3.2 Kaffrarian Succulent Thicket	94
3.4 Afromontane Forest	98
3.4.1 Knysna Afromontane Forest	100
4.0 Discussion	102
4.1 Soil nutrients and shrubland types	102
4.2 The role of soil moisture	107
4.3 Tension zones and chorological complexity	107
4.4 Conservation	108
References	111

INTRODUCTION

The work by the late J.P.H. Acocks, "Veld types of South Africa" is a standard guide for most vegetation studies in this country. Acocks' (1953) concept of a veld type is an agro-ecological unit of vegetation ".... whose range of variations is small enough to permit the whole of it to have the same farming potentialities". He is to be commended for his brilliant and insightful overview of vegetation patterns in South Africa, and the production of a vegetation map which is of great value to both academic and applied ecologists. Unfortunately, Acocks' criteria for distinguishing veld types are never fully defined and often incorporate vague and untestable statements on history, utilization and dynamics (see also Martin and Noel, 1960). He completed his major work at a time when the assumptions of Clementsian dynamics were largely accepted. This allowed for the grouping of structurally and floristically unrelated types into a single veld type, due to assumed successional relationships. Furthermore, Acocks' groupings of units above the level of the veld type are often unsound: Knysna Forest (4)* is included as a Coastal Tropical Forest Type (cf. White, 1978), Valley Bushveld (23) as a Karroid Type (cf. Moll and White, 1978), while False Fynbos (70) and Fynbos (69) are placed in different units due to the former's presumed derivation from mountain grassland, thicket and forest.

Clearly the time is long overdue for a critical re-evaluation of certain veld type concepts. This is especially true for the Fynbos Biome (Kruger, 1978) where Acocks (1953) explicitly states that his system is inadequate. In this paper I present a syntaxonomic hierarchy of vegetation units focussing on the level of the order, which is roughly equivalent to a veld type (cf. Van der Muelen, 1979). I have used floristic, biogeographic, structural, dynamic and habitat criteria to formulate syntaxonomic concepts and to make testable hypotheses regarding their origins and interrelations.

This study was carried out in the Humansdorp region, towards the eastern limit of the Fynbos Biome. This area provides a microcosm of many Biome vegetation types, as well as types representative of adjacent biomes. In Marloth's (1923) words ".... conditions of existence of associations of plants (can) be studied nowhere better than the boundaries of the areas where they encounter another vegetation of different requirements".

* In this paper bracketed numbers refer to Acocks (1953) veld type number.

In addition to clarifying syntaxonomic concepts above the level of the community, I expand on the physical and historical environment of the study area and thus provide the setting for future papers on community characterization and dynamics (Cowling, 1982 a-d), biogeography (Cowling, 1982 e), diversity relations (Cowling, 1982 f), growth form distribution (Cowling and Moll, 1982; Cowling and Campbell, 1982 a) and direct gradient analysis (Cowling and Campbell, 1982 b).

The scheme outlined below must, after Acocks' (1953) early work, be regarded as a second approximation (cf. Poore, 1962). I believe that it will provide a hypothetical framework which can be refined or rejected in future years.

1.0 THE STUDY AREA

The study area is in the Humansdorp region of the south eastern Cape (Fig. 1). The eastern Cape comprises a complex tension zone where elements of the Cape, Karoo-Namib, Afromontane and Tongaland-Pondoland phytochorological regions meet and combine to form a bewildering variety of vegetation types (Werger, 1978; Goldblatt, 1978; Gibbs, Russel and Robinson, 1981; White, 1982). A combination of a transitional and variable climate, complex topographical and geological patterns and species assemblages of diverse phytochorological affinities has resulted in communities highly vulnerable to the destabilizing influences of settled agriculture (Liebenberg, 1945; Trollope, 1980; Gibbs Russel and Robinson, 1981), resulting in the invasion and thickening up of weedy species (for a review see Trollope, 1970).

Few plant ecological studies have been undertaken in the eastern Cape in the last two decades, and none in the study area. A check-list for the Humansdorp district has been published (Fourcade, 1941). There are short descriptions of fynbos and thicket communities near Port Elizabeth (Olivier, 1977) and thicket communities in the Sundays River valley (Archibald, 1955; Penzhorn and Olivier, 1974; Olivier, 1981; Taylor and Morris, 1981). Acocks (1953) recognised three veld types in the study area: False Fynbos (70) is mapped as covering most of the region with tongues of Valley Bushveld (23) extending up the Gamtoos River valley and Alexandria Forest (2) occurring along the coast as far as Jeffreys Bay (cf. Fig. 3).

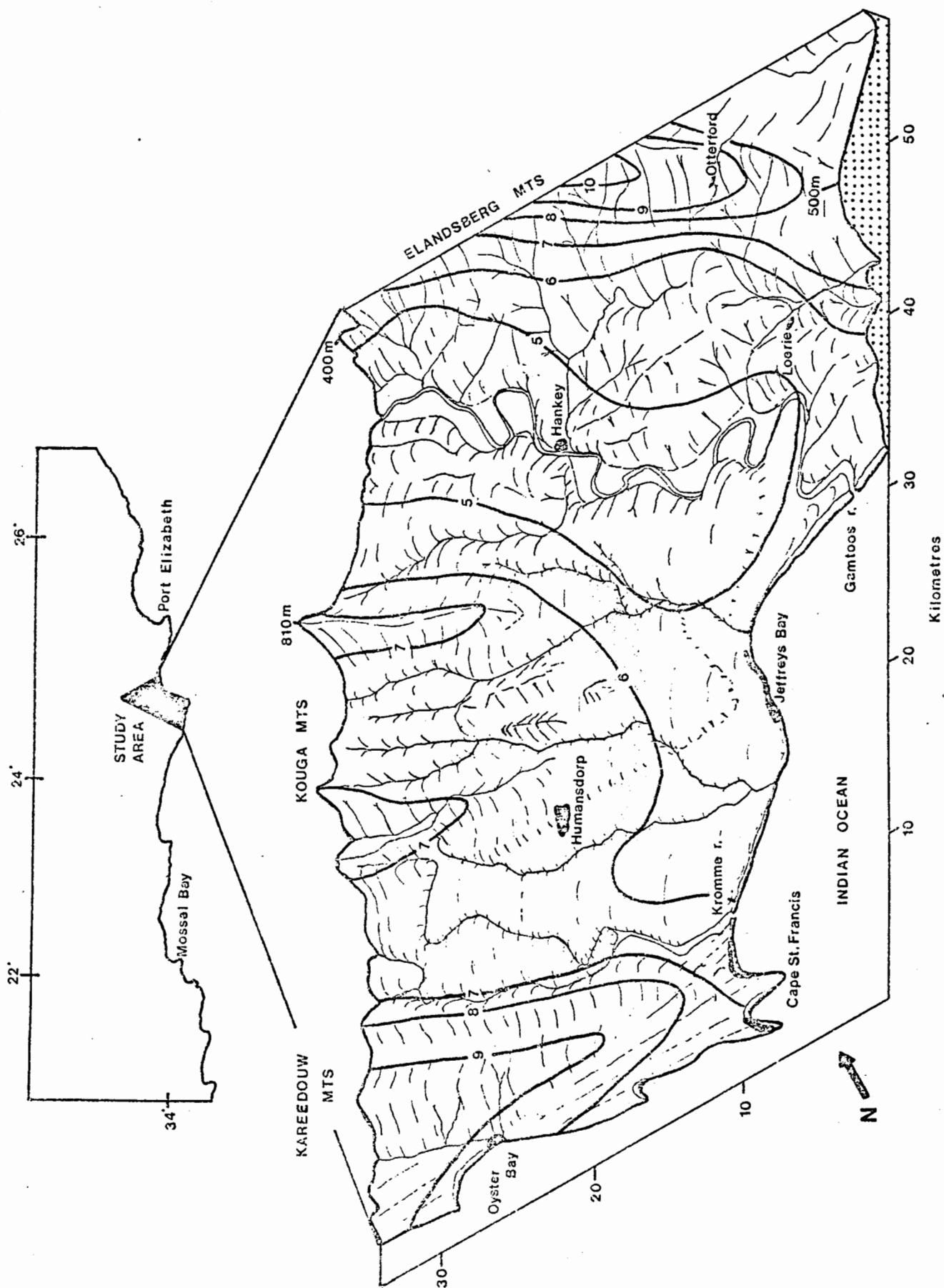


Fig. 1. Location, topography and isohyets of the study area.
Isohyets from 1 : 250 000 Average annual rainfall series.

1.1 Physiography

The study area has both physiographic elements of the southern Cape coastal region: the rugged quartzite mountains of the Cape Folded Belt and an undulating Coastal Foreland (Wellington, 1955) stretching from the mountain pediments (approximately 300 m) to the present shoreline (Fig. 1). The wide alluvial valley and braided course of the Gamtoos River (Fig. 1) is a feature more typical of the south eastern Cape.

The dominating feature of the landscape is the Great Winterhoek range culminating in the Cockscombe peak (1 750 m). This range forms the eastern end of the inland Swartberg-Baviaanskloof axis. East of the Gamtoos River a subsidiary range, with a more south easterly trend, is known as the Elandsberg. The coastal axis of the Folded Belt is represented by the Kareedouw mountains which terminate in the study area as two planed parallel anticlines which jut into the sea at Cape Seal and Cape St. Francis. The only other mountain area is the Klipfontein range (300 - 400 m) north-west of Humansdorp, which is the eastern termination of the Kouga mountains.

The Coastal Foreland comprises a plain which cuts across all geological formations (Fig. 2). In the southern Cape the coastal plain has been interpreted as an early Tertiary (Eocene) surface (peneplain) which slopes at a gradient of 1° from approximately 1 000 m in the mountain foothills (Du Toit, 1966; Haughton *et al.*, 1937). In the study area the plain forms gravel-covered terraces above the deep and narrow v-shaped incised valleys. Away from the mountains, the plain is more extensive and in places, especially where the underlying material is of the Uitenhage Group, is covered by a veneer of limestone and marine gravels of the Alexandria Formation (Fig. 2).

King (1972) argues that, up to an elevation of about 350 m the coastal plain in the south east Cape is one of marine abrasion. Uplift due to monoclinal tilting of the sub-Miocene surface along an east-west axis resulted in a Pliocene marine transgression. Marine sediments of the Alexandria and Bredasdorp Formations were deposited in a transgressive phase and redistributed in the regressive phase (King 1972, 1978). The plain is therefore interpreted as a "composite marine and continental bevelled surface" (Heydorn and Tinley, 1980) and not simply a subaerially formed peneplain.

The geomorphology of the coastal foreland is dominated by planation forms related to a descending sequence of high sea levels (Butzer and Helgren, 1972). The most striking surface occurs immediately north of Humansdorp (Fig. 1) on the 200 m contour - this is the Coastal Platform (largely gravel-capped in the study area). Other surfaces and

terraces can be seen in places at 100 m, 60 m and 30 m (Butzer and Helgren, 1972).

The dominant feature of the coastline is the series of half-heart bays (Silvester, 1960; Heydorn and Tinley, 1980). They are usually formed as a result of the seaward truncation of resistant rocks (T.M.G. quartzite) and the greater erosion of softer rocks to the north. This results in asymmetric east-facing bays in which the rock outcrops form headlands at the apex of the short part of the curve (e.g. St. Francis Bay, Fig. 1). Recent deposits of siliceous sands accumulate against the long curve of the half-heart embayments (Heydorn and Tinley, 1980).

The most extensive dune-fields in the study area occur between Oyster Bay and Cape St. Francis and also near the Gamtoos River mouth. In the former region fixed dunes have been reactivated, possibly in the recent past (Keet, 1936). Transverse dunes, aligned at right angles to the prevailing wind direction, predominate in the reactivated dune-fields. Fixed dunes are aligned parallel to the direction of the prevailing (SW) winds and are termed linear hairpin dunes (Heydorn and Tinley, 1980). These are essentially parabolic dunes, the noses of which have been blown out, and must have been formed under a wind régime considerably stronger than present (Tinley, pers. comm.).

The Gamtoos River has its source in the mountains of the Great Karoo. After breaching the Groot Winterhoek range it enters the study area in a deep meandering valley and flows in a general south-easterly direction to the sea (Fig. 1). The other major rivers – the Kromme and the Kabeljous – flow in strike valleys which are deeply incised into the coastal plain.

1.2 Geology

The oldest rocks in the region belong to the late Pre-Cambrian Cango Formation of the Malmesbury Supergroup. They occur in a faulted block truncating the southern limbs of the Elandsberg range with down-faulted Uitenhage beds to the south (Fig. 2). The lower beds consist of phyllites with two thick horizons of limestone; the upper beds are principally arenaceous consisting of felspathic grits, small pebbled conglomerates and quartzites (Haughton et al., 1937). In the field it is difficult to distinguish the last mentioned from T.M.G. quartzites.

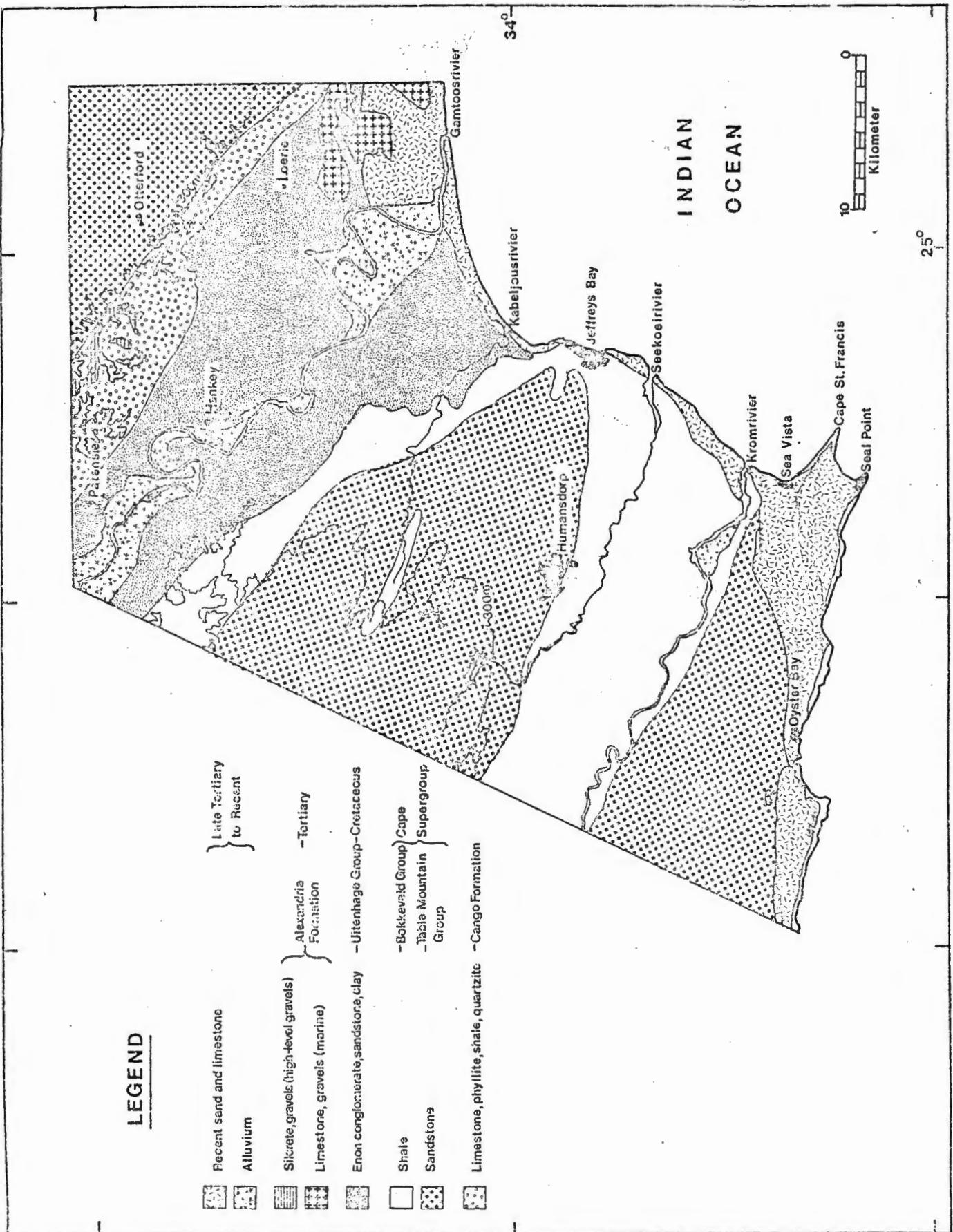


Fig. 2: Geological map (after Haughton et al., 1937).

Rocks of the Cape Supergroup predominate in the study area. These were laid-down in a basin depository on a planed surface of Malmesbury-Cango rocks in a largely marine environment in late Silurnian and Devonian times (Rust, 1967). Folding was initiated 200 - 300 m.y. during the Cape-Karoo orogeny.

Table Mountain quartzites and sandstones comprise the mountain ranges in the area but also underlie considerable portions of the coastal plain (Fig. 2). The beds are highly folded, usually assymetrically with steeper dips to the north, and overfolding is common. They are made up of well jointed, massive quartzitic sandstones; there are no conglomerates or basal shales. Shale bands sometimes occur near the top of the group (Haughton et al., 1937).

Bokkeveld beds are found in a narrow wedge on the coastal plain (Fig. 2). They are argillaceous throughout and composed of soft, yellowish to greenish grey shales (Haughton et al., 1937).

In the late Jurassic times (140 m.y.) faulting occurred in the southern Cape contemporaneous with the separation of the African plate from the South American plate (Sclater et al., 1977). This faulting, which exposed pre-Cape rocks in the study area, also created minor tectonic valleys into which Cretaceous fluvial, estuarine and shallow marine sediments were laid down (Du Toit, 1966). These are the sediments of the Uitenhage Group which occur extensively in the Gamtoos River valley, where they are bounded in the north by the fault plane and rest unconformably on Bokkeveld rocks in the south (Fig. 2). Only Enon beds are present although there is some evidence of Variegated Marls near Loerie (Haughton et al., 1937). The variability of these deposits has been stressed by Du Toit (1966). In the lower Gamtoos valley coarse grained conglomerates and sandstones, deposited under fluvial conditions, are the predominant rocks. Along the north side of the river and towards the mouth the beds become finer, passing into fine sandstones with reddish marls and grey sandy clays (Haughton et al., 1937). These are well displayed in the cliffs on both sides of the Gamtoos mouth.

Tertiary deposits include the subaerial high level gravels and marine deposits of the Alexandria Formation (Fig. 2). The former, which abut against steep mountain slopes, have probably originated mostly as scree or talus material (Haughton et al., 1937) resting on an early Tertiary surface (King, 1972). Silification took place subsequent to deposition, probably during an arid climatic phase (Du Toit, 1966).

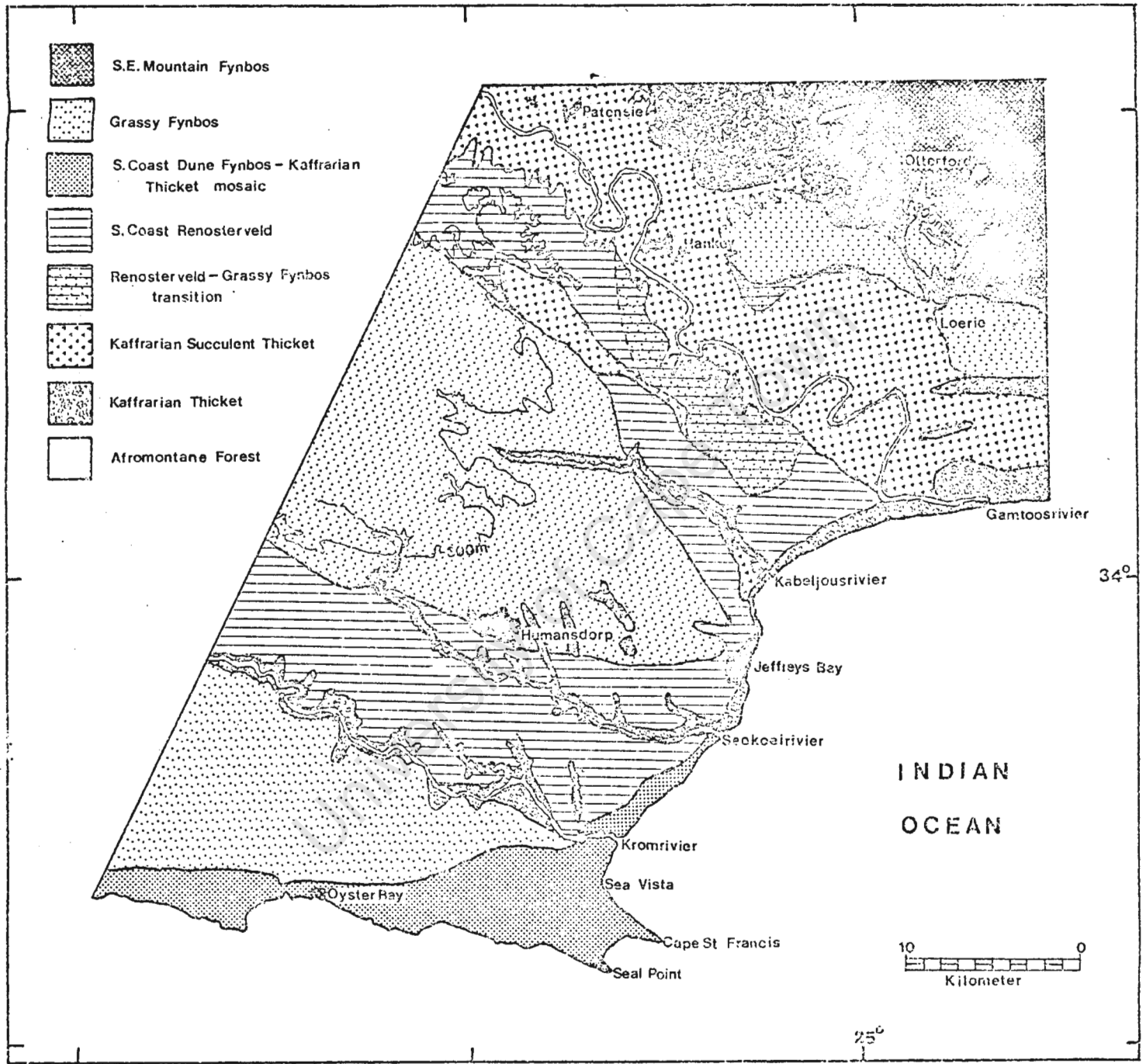


Fig. 3. Vegetation map. Units mapped are orders (see Table 3).

The marine deposits of the Alexandria Formation are of Pliocene age (King, 1972). They occur on the northern bank of the Gamtoos, overlying the Uitenhague beds (Fig. 2) and have probably been removed from the remainder of the coastal plain by Quaternary subaerial denudation (King, 1972). The beds are usually covered by white tufaceous limestone and sand (Haughton *et al.*, 1937).

Recent and Quaternary deposits occur as alluvium in the Kromme and Gamtoos valleys and as dune sands along the coast (Fig. 2). In the latter area deposits of calcrete outcrop between the longitudinal dune ridges and also immediately behind the dunes along the Jeffreys Bay coast.

1.3 Climate

A discussion of the climate is necessarily hampered by a lack of climatic data, particularly temperature data, which are recorded only at Cape St. Francis. These data were extrapolated to other stations on the coastal plain (Oyster Bay, Humansdorp, Jeffreys Bay). At Otterford temperature data from the nearby Van Stadens station (452 m) were used and those of Uitenhague (108 m) for Hankey. Corresponding stations are physiographically matched. Climate diagrams are shown in Fig. 4.

1.3.1 Seasonal climatic controls

The climate in the study area is warm temperate. The climatic régime is dominated by an alternating succession of east-moving cyclones budded off from the circum-polar westerlies, and high pressure anti-cyclones which ridge in behind the lows (Jackson and Tyson, 1971; Schulze, 1972).

The frequency and intensity of cyclonic fronts is greatest in winter as a result of the northward migration of the pressure belts; the weather is cool and much rain falls. In summer a strengthening and southwards migration of the South Atlantic high pressure cell effectively blocks westerly cyclones reaching the south western Cape resulting in a markedly reduced precipitation (Mediterranean-type climate). This effect is not felt so strongly along the southern Cape coast where a considerable amount of summer rain falls.

Summer precipitation is usually associated with the approach of cool post-frontal air from the south west, moving over a relatively warm ocean, as an anti-cyclone progresses north eastwards along the coast, or as a result of cut-off lows (Anon., 1942; Schulze, 1972).

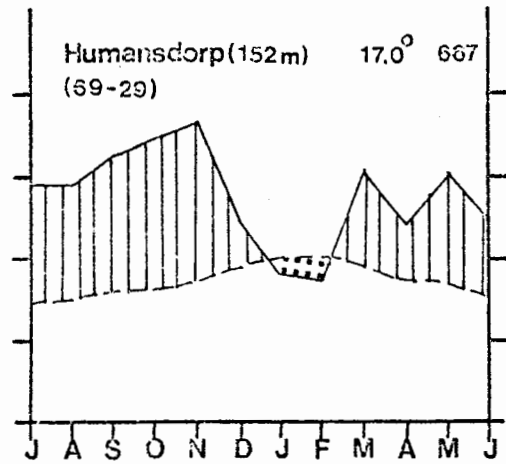
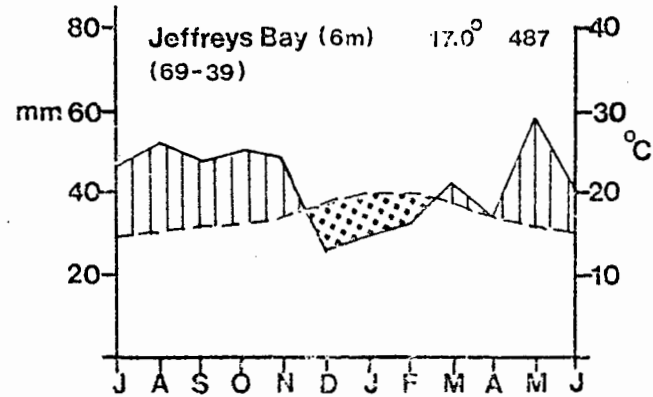
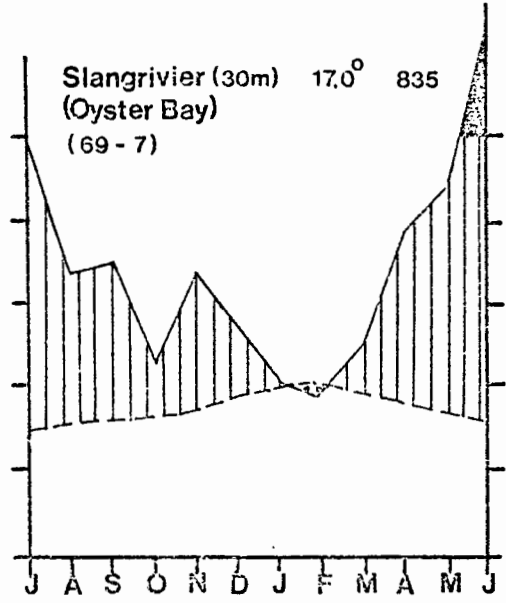
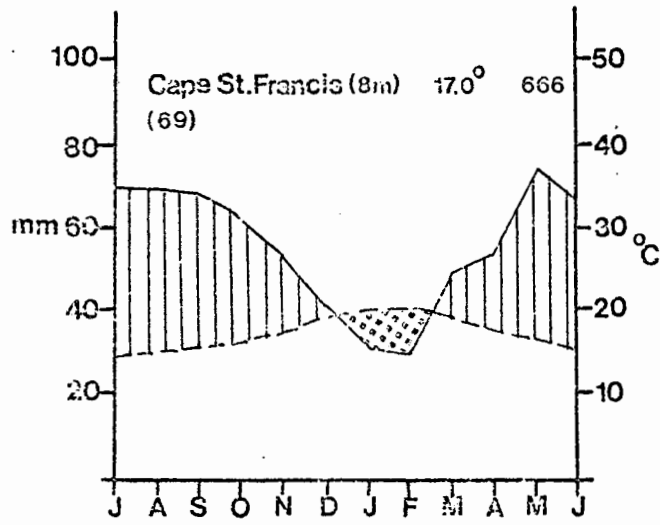
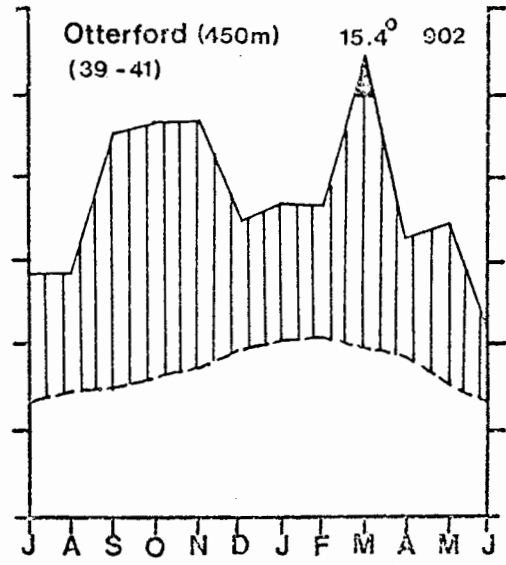
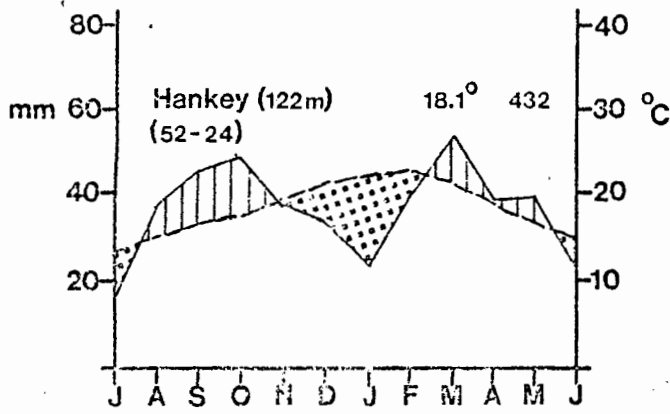


Fig. 4. Walter-Lieth climate diagrams. Data from Anon.(1942) and Weather Bureau (1954).

1.3.2 Climatic classification

The study area has a climate transitional between Köppen Cfb and Csb climates (cf. Schulze and McGee, 1978). The temperature régime is warm temperate and rain may fall at any time of the year although the three summer months (Dec. – Feb.) are always driest (Fig. 4). Three climatic types can be recognised at the mesoclimatic level:

- (i) Coastal plain subhumid climate: Occurs on the coastal plain and lower slopes of the Elandsberg where the annual rainfall ranges from 500 to 800 mm (Fig. 1) (e.g. Oyster Bay, Humansdorp, Cape St. Francis). Along the coast it is cooler due to the tempering effect of onshore winds. To the west of the study area it merges with a Tsitsikamma humid climate and in the east, near Jeffreys Bay, with the valley climate (see below).
- (ii) Semi-arid valley climate: Restricted to the low lying areas of the Gamtoos and Seekoei rivers where the annual rainfall is less than 500 mm (Fig. 1). As with other river valleys in the south eastern Cape, the climate is much drier and more variable than conditions on the adjacent mountains and interfluves (Anon., 1942; Lieberberg, 1945).
- (iii) Humid coastal mountain climate: This is the climate of the moist, sea-facing slopes of the Elandsberg mountains where annual precipitation is in excess of 800 mm (Fig. 1). The climate is equable with sufficient rain throughout the year; it is the forest climate of the George-Knysna-Tsitsikamma area (cf. Phillips, 1931).

Below, I discuss briefly some climatic features with reference to the climatic types listed above:

1.3.3 Winds

The usual wind pattern during the path of a cyclonic front is the backing from NE to NW (often associated with an increase in temperature if "berg winds" persist) and then from W to SW as the front passes (Anon., 1942). The latter condition is usually accompanied by high winds, cooler weather and rain. With the onset of anti-cyclonic conditions the wind backs from S to E, the skies clear and the weather warms up. At the equinoxes there are often strong southerly winds and flood conditions resulting from "cut-off" low pressure cells in the interior advecting cool, moist air from anti-cyclones off the coast (Heydorn and Tinley, 1980).

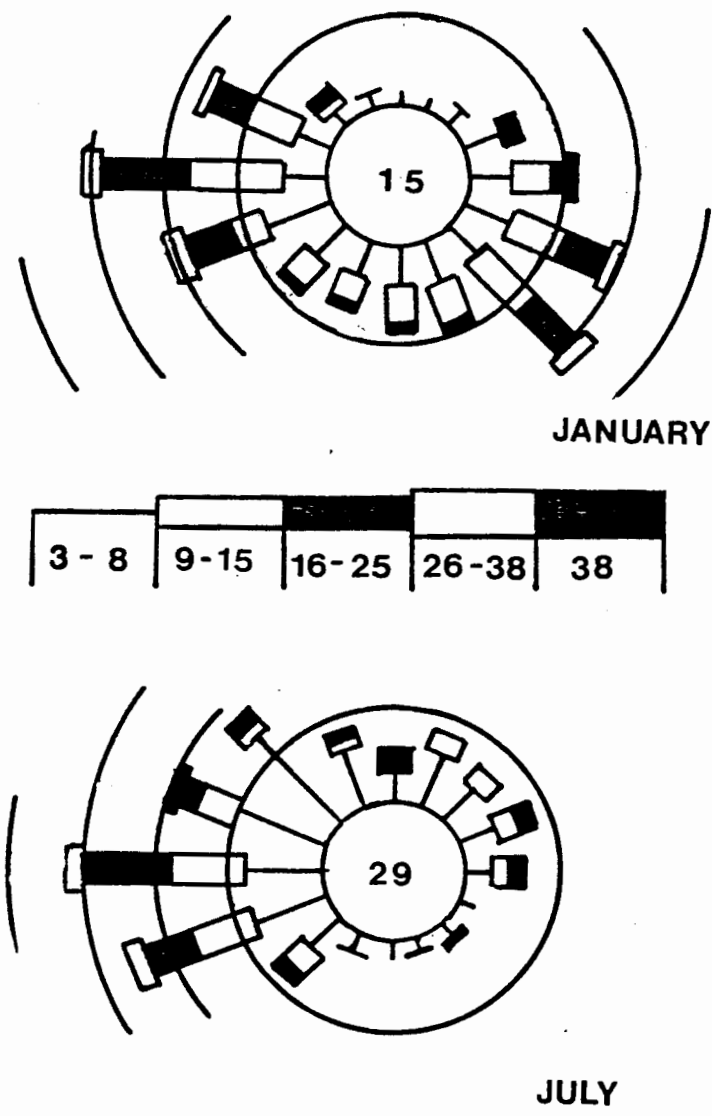


Fig. 5. Summer and winter wind roses for Port Elizabeth.
Areas represent 5% intervals. Percentage calms within the circle.
Data from Schulze (1972)

Wind roses for Port Elizabeth are shown in Fig. 5. The area is liable to strong winds and occasional gales at any time of the year. Specht and Moll (1982) observe that wind régimes on the Cape coast are much stronger than analogous areas in Australia and that this has implications for plant growth in the former region due to increased evapotranspiration. Along the southern and south eastern Cape coast the calmest period is in the autumn months (March - May) while spring (Sept. - Nov.) is the windiest (Anon., 1942). The prevailing wind direction is from W to SW while there is a significant increase in E and SE winds in summer (Fig. 5). Hot, dry and turbulent berg winds, which are composed of subsidiary air masses draining seawards from the interior, have their highest frequency in the winter months (Tyson, 1964; Fig. 5). They are always accompanied by a sharp increase in temperature, giving rise to the anomalous situation where some of the highest temperatures (up to 38°C) are recorded in winter (Anon., 1942; Tyson, 1964; Louw, 1976). The wind régime shown in Fig. 5 is representative of the coastal plain climate. The valley climate is less susceptible to the cooling effect of summer sea breezes (E to SE) (Louw, 1976; pers. obs.). It is likely that the wind régime in the mountains differs in many aspects from that on the coast (H.T. Scharf, pers. comm.).

1.3.4 Precipitation

Most precipitation falls in the form of rain. Snow, associated with "cold snaps" in winter falls rarely on the mountains and then persists for only a few days (pers. obs.). Mists are important in the mountains where drizzle from S and SE winds can result in considerable precipitation (cf. Nagel, 1962). Sea (advection) fog is uncommon (average of 20 days per year at Port Elizabeth) and shows its greatest frequency in late summer (Anon., 1942; Heydorn and Tinley, 1980). There are no data for land (radiation) fog. Indications are that it is restricted almost entirely to the Gamtoos valley and occurs mainly in winter (May - June) (Anon., 1942; pers. obs.).

Mean annual isohyets (from 1:250 000 average annual rainfall series) are shown in Fig. 1. Precipitation decreases in a north easterly direction from Oyster Bay to the Gamtoos valley and then increases sharply up the Elandsberg range. Mean annual rainfall for eight stations ranging in elevation from 61 m on the floor of the Gamtoos valley to 535 m in the Elandsberg, showed a linear increase of rainfall with elevation (mean annual rainfall = $228,4 + 0,8031 \cdot \text{altitude}$; $r = 0,93$; $p < 0,001$).

Rainfall distribution varies from sub-mediterranean on the coast (Dec. – Feb. dry period) to bimodal in the valley climate (additional June – Aug. dry period). In the Elandsberg prolonged dry periods are probably rare. Using the difference between Thornthwaite's index of potential evapotranspiration and rainfall, Bond (1980a; 1981) has shown that semiarid and subhumid climates in the southern Cape constant rainfall region have an effective moisture régime that is unequivocally mediterranean as typified by winter moisture surpluses.

Low intensity orographic rain predominates throughout the year although pre-frontal thunderstorms are occasional in summer. Falls of up to 120 mm per day have been recorded during cut-off low conditions (see above) (Anon., 1942). Heaviest downpours are associated with post-frontal SSW and S winds. The valley area receives little frontal rain (W to SW winds) (pers. obs.).

1.3.5 Temperature

Mean annual temperatures are shown in the climate diagrams (Fig. 4). Generally the temperature régime for the coastal plain and mountains is equable while in the Gamtoos region diurnal and annual variations are greater. Frost is uncommon. Cold snaps occur in winter when strongly developed cold fronts are followed by an anticyclone which advects cold polar air landwards (Schulze, 1972). Hot spells are correlated with persistent berg winds (usually in spring) and with warm summer anticyclones.

River valleys in the south eastern Cape show great annual and daily extremes in temperature (Anon., 1942). At Uitenhage, in the Swartkops river valley, the highest mean daily maximum is recorded in February ($29,1^{\circ}\text{C}$) and the coldest in July ($5,9^{\circ}\text{C}$); corresponding temperatures for Cape St. Francis are $22,8^{\circ}\text{C}$ and $10,1^{\circ}\text{C}$ respectively (Anon., 1942). This pattern is further illustrated in Fig. 6 which shows the monthly mean maximum and minimum temperatures at Port Elizabeth Airport (climatically similar to Cape St. Francis) and Uitenhage, measured over a period of two years (Louw, 1976). The minimum mean daily range at Uitenhage is $12,2^{\circ}\text{C}$ (Nov.) and the maximum $15,5^{\circ}\text{C}$ (June). Corresponding figures for Cape St. Francis are $4,9^{\circ}\text{C}$ (March) and $8,4^{\circ}\text{C}$ (June). The months with the highest and lowest mean absolute maxima at Uitenhage are February ($39,2^{\circ}\text{C}$) and July ($-0,4^{\circ}\text{C}$) respectively; corresponding data for Cape St. Francis are April ($29,7^{\circ}\text{C}$) and August ($5,0^{\circ}\text{C}$) (Anon., 1942). There are no detailed temperature data for the mountain climatic type. H.T. Scharf (pers. comm.) has

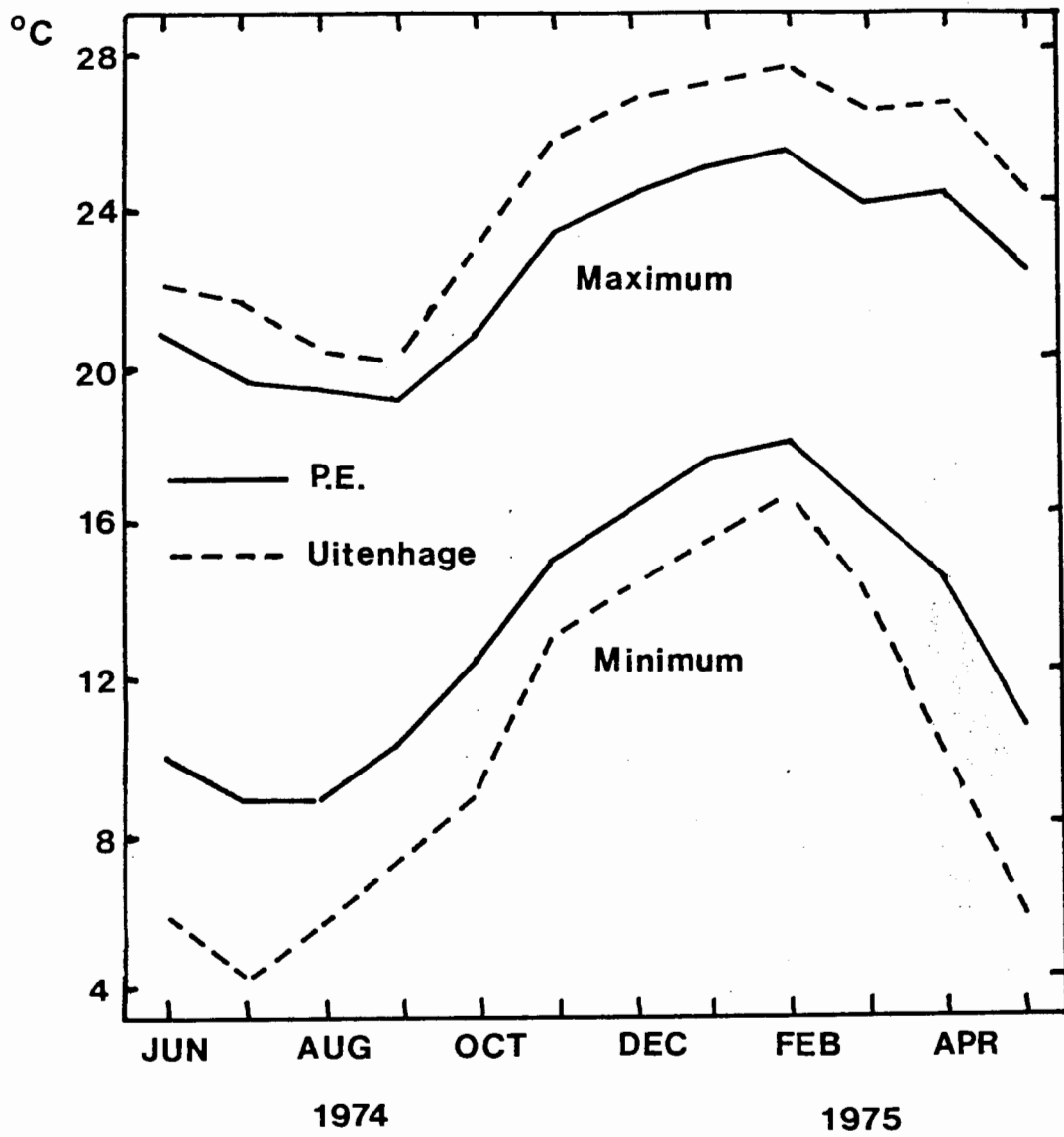


Fig. 6. Mean monthly maximum and minimum temperatures at Port Elizabeth Airport and Uitenhage. Data from Louw (1976).

measured an environmental lapse rate of $0,6^{\circ}\text{C}$ per 100 m in the Great Winterhoek mountains near Uitenhage.

1.3.6 Solar radiation

Solar radiation has an important bearing on ecological studies (Schulze and McGee, 1978) as the effects of terrain slope and aspect on radiant energy régimes lead to corresponding variation in soil moisture status (Holland and Steyn, 1975; Holland *et al.*, 1977; Granger and Schulze, 1977) and pedogenesis (Garland, 1979). Fig. 7 shows the influence of topography on solar radiation at 34°S (data from Schulze, 1975). During summer there is little difference in potential radiation on all slopes and aspects. At the equinoxes there is a trend for increased radiation on steeper north slopes and a more marked decrease in radiation on steep south slopes. In the southern winter, radiation is strongly affected by a lower sun azimuth and steep north slopes receive markedly more radiation than steep south slopes (Fig. 7).

1.4 Soils

The diversity of parent material and the complex topography of the study area combine to produce complex soil patterns. Furthermore, a sequence of late Cainozoic changing environmental factors including tectonic deformation, eustatic fluctuations of sea level and fundamental changes in climate and vegetation have affected pedogenesis in a number of ways (Butzer and Helgren, 1972). Information on soils in the Fynbos Biome is given by Lamprechts (in Boucher, 1978; 1979), Bond (1981) and in a comprehensive review for the mountains of the biome by Campbell (1982a). There are no published data on the soils of the study area.

It is not within the scope of this study to produce a comprehensive survey of soils. I restricted my observations to augerings (where possible) in sample plots and notes from roadside cuttings. Chemical characteristics are generalised from the results of 101 analyses of soil samples collected at approximately 15 cm depth (see Methods). Results of these analyses are shown in Fig. 8. These data are used for comparisons among substrate and vegetation types and do not adequately reflect nutrient régimes. The term "soil fertility" reflects the nutrient requirements of common crop and pasture plants. Soils are classified according to the system of MacVicar *et al.* (1977). I describe the soils of each parent material separately and discuss briefly vegetation-soil patterns. A brief characterization of the major vegetation types referred to in this section, is presented in Table 3.

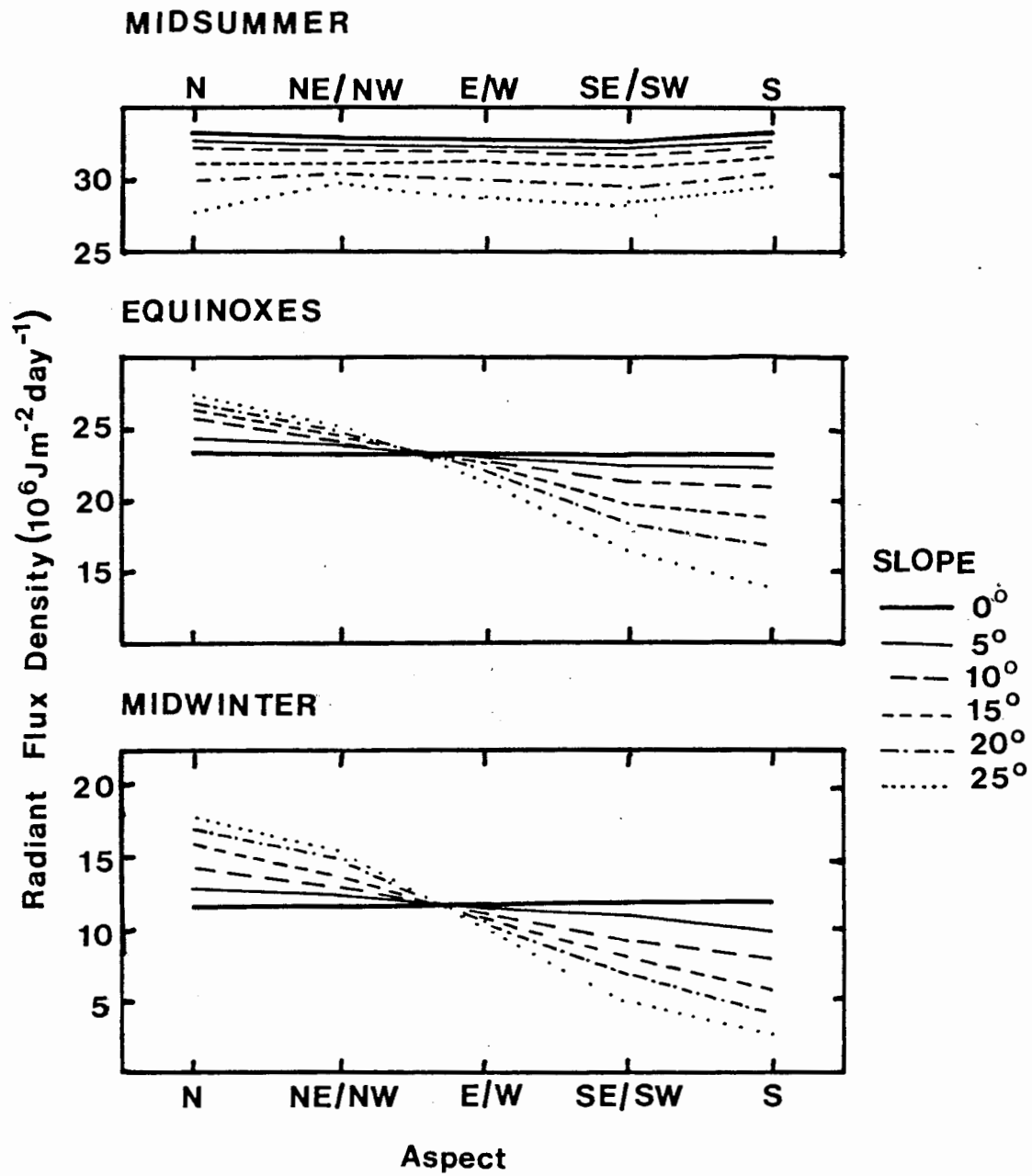


Fig. 7. Influence of topography on solar radiation.
Daily incoming radiant flux densities on sloping terrain as a function of slope, aspect and season, for cloudless days at 34°S .
Data from Schulze (1975).

Examples of profiles of the soil forms and their correlation with the FAO and USDA systems are shown in MacVicar *et al.* (1977). Correlation and regression studies of soil, other environmental, and floristic variables are given in Cowling (1982 a-g).

1.4.1 Cango Formation

I restrict my discussion to the soils derived from limestones and phyllites near the Kleinfontein quarry below Otterford (Fig. 2). The soils are deep (1 – 3 m) with uniformly red, apedal subsoils (Hutton form). Topsoils are slightly acid to neutral loams, rich in exchangeable bases (S value : 14 – 28 meq %) especially calcium. Values for total nitrogen are high but available phosphorus is fairly low (4 – 10 ppm). Soils are well-drained and support dense thickets.

1.4.2 Table Mountain Group

Soils derived from sandstones and quartzites of the T.M.G. are mostly infertile and invariably support fynbos vegetation (Fig. 8). Kruger (1979) has generalised the fynbos soils of the quartzitic fold ranges as greyish, acid, shallow sands to sandy loams with low base saturation (see also Lamprechts, 1979). He also stressed the importance of podzolization as a pedogenic process in fynbos soils. Recent work by Bond (1981) and Campbell (1982a) has shown that mountain soils are: much deeper than usually assumed (the difficulty of excavating rocky profiles cannot be overlooked!); that red and yellow-brown profiles are common; and that true podzols are rare. Campbell (1982a) has demonstrated a west-east gradient of increasing clay fraction and finer sand fraction, and increasing exchangeable bases in the mountains of the Fynbos Biome. In the south eastern Cape, mountain soils are generally more fertile than the southern and western Cape.

In the mountains a combination of steep topography and slow weathering of resistant rocks usually results in lithosols on steep slopes and deeper colluvial deposits in valley fills, pediments and talus slopes (Lamprechts, 1979). Soil patterns in the Elandsberg mountains are complex and similar to those on the seaward slopes of the Outeniqua mountains (Bond, 1981). On steep north-facing slopes and ridges, soils are predominantly litholic (Mispah and Glenrosa forms) while Cartref form (Amabele series Cf 20), with an eluvial (E) horizon on a poorly developed illuvial B horizon, predominates on rounded anticlinal ridges and gentle slopes. Deeper Clovelly and Hutton forms occur at lower altitudes on talus slopes and pediments; Oakleaf (low clay content in B horizon) and Fernwood forms are less common. Mountain fynbos occurs on these soils. Valley fills and minor

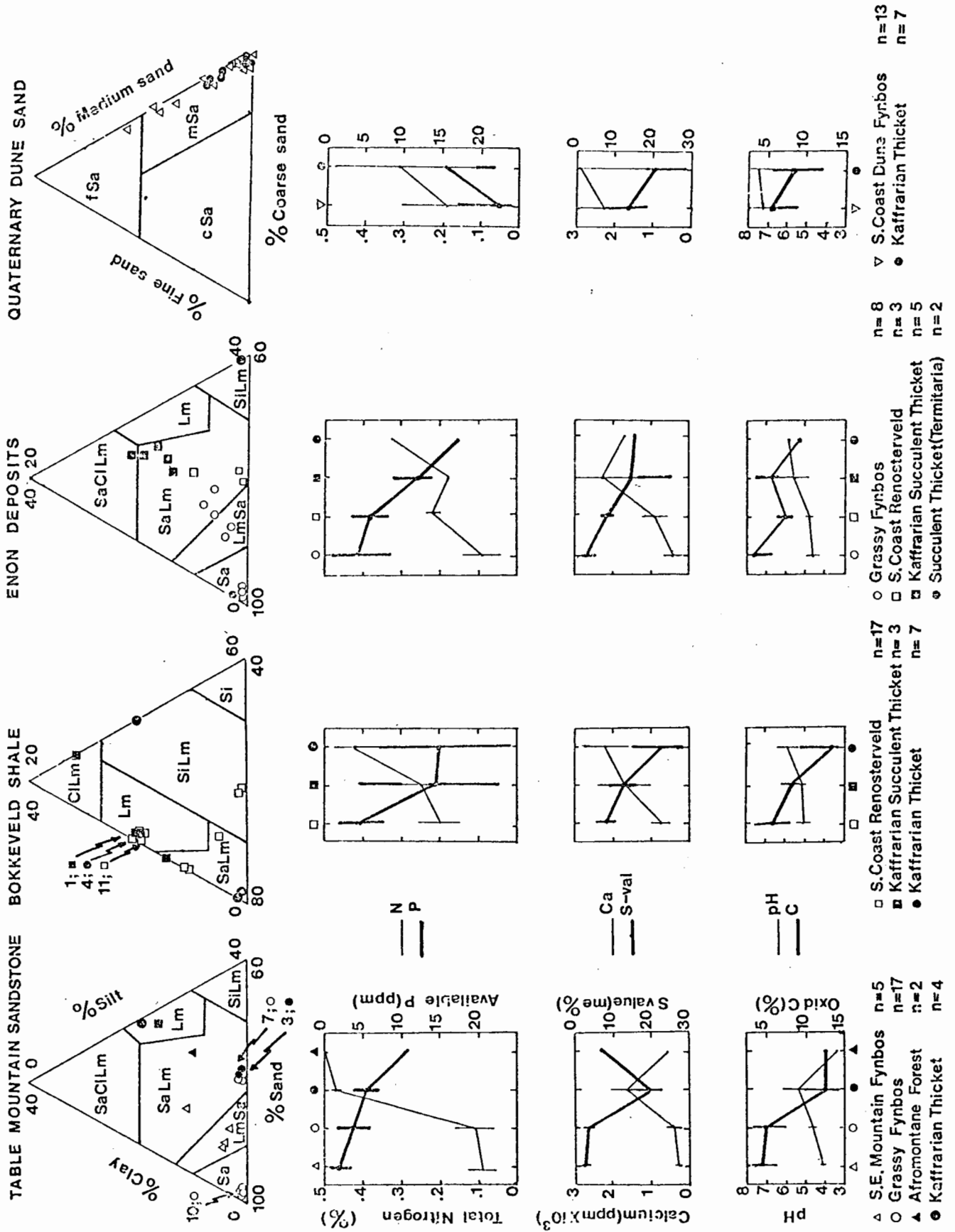


Fig. 8. Soil analyses for communities on different parent materials. Chemical data shown as the mean \pm standard deviation.

colluvial-alluvial basins have deep ($> 1,5$ m) Oakleaf (Koedoesvlei series Oa37) soils with a high clay content in the B horizon and pronounced organic staining in the upper soil layer. These soils have good moisture retaining properties and support forest. No true podzols were seen.

Mountain fynbos soils are very strongly acid (pH 3,9 – 4,2), loamy sands to sandy loams and have low levels of all major nutrients (Fig. 8). Forest soils are very strongly acid loams to sandy loams, rich in oxidizable carbon. A strong correlation between carbon and other nutrients (see Cowling, 1982d) suggests that the relatively high fertility of these soils (Fig. 8) depends largely on organic enrichment from plant remains in the soil.

T.M.G. soils on the coastal forelands differ from the mountain soils in that they are mostly colluvial, deeper and somewhat more fertile. Lateritic hardpans of ferricrete, overlain by colluvial gravels and sands are found on the Coastal Platform north of Humansdorp and south of the Kromme river near Oyster Bay. These may well correlate with palaeosols described elsewhere in the southern Cape by Helgren and Butzer (1977) although I did not excavate profiles below the ferricrete to confirm this.

A dominant feature of the Coastal Platform to the north of the Klipfontein mountains is a capping of sub-rounded to sub-angular colluvial gravel (1 – 1,5 m) with reworked ferricrete, and set in a reddish sandy loam matrix. These soils are best described as a dystrophic Hutton form (stony phase) although the rooting layer is mainly confined to greyish sandy loam topsoil. On the upper slopes of anticlinal remnants (Klipfontein mountains) soils are Mispahs and Glenrosas while deep Hutton soils, supporting thicket vegetation, in contrast to grassy fynbos elsewhere, occur on stable, north facing screes and talus slopes. The anticline to pediment catena on the southern flanks of the hills is Mispah → Glenrosa → dry Fernwood → wet Fernwood and Longlands on the pediment. The last two mentioned soils are underlain by a ferricrete hardpan, are seasonally waterlogged, and support predominantly herbaceous vegetation (restioid grassland). Weakly developed podzols are occasionally found: Houwhoek form on the lower slopes and Lamotte form in depressions on the pediment.

A more or less similar catena exists on the southern sides and valleys of the planed folds south of the Kromme river (see Fig. 1). A schematic soil and vegetation catena is shown in Fig. 21. Deep sands with a strongly developed bleached (E) horizon (Constantia form) occur on north slopes above the Kromme river.

Along the valley walls of the Kromme and other rivers there are a number of slope breccias and colluvial deposits usually on concave slopes. Soils are often deep, sometimes comprising an angular rock rubble in a matrix of greyish to brownish organic enriched loam to sandy loam. Deep red Hutton soils are also found. These soils are associated with thicket vegetation.

Grassy fynbos soils are infertile, strongly acid (pH 4,2 – 5,1) sands, loamy sands and sandy loams; thicket soils are moderately acid (pH 4,8 – 6,5) loams to sandy loams whose improved fertility status is probably due to organic matter enrichment (Cowling, 1982b) (Fig. 8).

1.4.3 Bokkeveld Group

Soils derived from the Bokkeveld shales can be grouped into two classes. The first class comprises the shallow duplex soils of the level interfluvies below the Coastal Platform (see Fig. 1). These soils are at a relatively youthful stage of development as evinced by the poorly developed B horizons. Subsoils are clay-rich lithocutanic (sometimes pedocutanic) horizons which have developed in situ; topsoils (0,15 – 0,3 m) are sandier (loams to sandy loams) and typically demarcated by a stone line, indicating colluvial origin. The Glenrosa form (Williamson series GS 16) is predominant although the Swartland form (Breidbach series SW 12) is commonly found. As a consequence of the duplex structure these soils become waterlogged in winter, especially where run-off is minimized by a low relief and good vegetal cover. Under these conditions they support grasslands but in regions of steeper relief and where overgrazing has resulted in prolonged soil exposure and capping, and topsoil truncation, renosterveld is the predominant vegetation.

The second group comprises deeper, well-drained soils of the slopes and bottoms of the river valleys. They are invariably thicket covered, have a superficial enrichment of organic matter and a high water-holding capacity. Common forms are Clovelly and Hutton although Glenrosas do occur where fractured bedrock outcrops along valley slopes. In the last-mentioned situation it is difficult to estimate effective soil depth since roots can penetrate down soil-filled fissures in the bedrock. Slope breccias are also common in the valley topography. A schematic soil-vegetation catena is shown in Fig. 29. Renosterveld soils are strongly to moderately acid sandy loams to loams, considerably more fertile than fynbos soils (Fig. 8). Thicket soils are fairly fertile, moderately acid loams, sandy loams and clay loams (Fig. 8).

1.4.4 Uitenhage Group

The variable nature of the Enon beds in terms of the mode of deposition and resultant parent material is fully expressed in the complexity of soil types associated with the Uitenhage Group. A rough distinction can be made between soils derived from parent materials deposited under lacustrine and estuarine conditions and those deposited under fluvial conditions (cf. Haughton *et al.*, 1937; Du Toit, 1966). The former are fine-grained rocks (mudstones, shales, soft sandstones) which are strongly weathered giving rise to deep uniformly yellow-brown to red soils (Clovelly, Hutton and Griffin forms). These soils are well-drained and support thicket.

The fluvial Enon sediments are massive coarse-grained conglomerates and sandstones; soil structure and fertility status are broadly similar to those derived from the sandstones and quartzites of the T.M.G. Soils of the conglomerates of the coastal plain and southern margin of the Gamtoos valley are Oakleaf form (stony phase). Topsoils are shallow (0,1 - 0,3 m) and the rooting zone does not usually penetrate the underlying conglomerate. Above Hankey and Loerie shallow topsoils overlie coarse false-bedded sandstones (Glenrosa form); deeper Cartref and Constantia forms, with bleached E horizons, are occasionally found on gently sloping ground and depressions. The boundaries of the thicket and fynbos communities (Fig. 3) in the area, correlate with the distribution of the two above-mentioned suites of soils.

Thicket soils are moderately acid, fairly fertile sandy loams to sandy clay loams (Fig. 8). Fynbos soils are texturally and chemically similar to T.M.G. fynbos soils, whereas renoster-veld soils are of intermediate fertility and similar to renosterveld soils on Bokkeveld shale (Fig. 8). They differ in being sandier and well-drained.

1.4.5 Recent dune sands

Soil patterns of the aeolian dune sands are comparatively simple and the various forms are strongly associated with dune topography. The parallel dune ridges have well-drained Fernwood form (Langebaan series FW 21). The climax vegetation is thicket although successional dune fynbos communities are prevalent today. On southern slopes of the dunes soils are organic stained to a depth of about 0,5 m. On drier, less densely vegetated north slopes the humus layer is often absent suggesting gravitational transport of soil surface material. Near Oyster Bay soil development has resulted in iron oxide coatings on the sand grains and these no longer qualify as regic sands: they are classified

as Clovelly form (Oranje series Cv 41) or more rarely Hutton form (Nyala Hu 41) and are probably allied to the Red Berea Sands (Heydorn and Tinley, 1980).

Soils of the dune valleys are mostly poorly drained owing to the presence of a calcrete hardpan. Deep seasonally waterlogged sands with an abnormal accumulation of organic matter predominate. These are classified as Fernwood form (Soetvlei series FW 41).

In some situations soft plinthic subsoils are found within 1,2 m of the surface and the soils are therefore classed as Longlands form. Lamotte form, showing a vesicular hardening in the B horizon, is occasionally found in dune hollows. The abovementioned suite of soils support predominantly herbaceous vegetation.

Where the calcrete is exposed or covered by a thin mantle of sand, the soil form is Mispah (Kalkbank series Ms 22) and the vegetation is dune fynbos. A schematic soil-vegetation catena in the dune topography near Cape St. Francis is shown in Fig. 25.

Dune soils are neutral to alkaline medium sands. Fertility status is high but the availability of nutrients such as phosphorus may be limited by high pH values (cf. Brady, 1974) (See Fig. 8).

1.4.6 Alluvium

Stratified alluvium (Dundee form) occurs in the lower reaches of the Kromme and Gamtoos rivers. I sampled alluvial soils at one site in the Gamtoos valley near Hankey. They support thicket and are deep (>1,5 m), neutral loams and extremely fertile (85 to 90 ppm available phosphorus).

1.5 Historical land use

The past two decades have seen much research on the prehistory of the south and south eastern Cape (Klein, 1974; Deacon and Brooker, 1976). These studies have made an important contribution to our understanding of primitive man from Middle to Late Stone Age cultures and also on environmental changes during the time spanning these cultures (about 100 000 years ago to historical times). In this section I focus on patterns of land use associated with indigenous peoples prior to their displacement by European settlers and on settled agricultural practices associated with the latter peoples. I concentrate on those forms of land use which contributed to recent gross vegetational changes in the study area.

The aboriginal people encountered by the first Europeans in the Humansdorp area were terminal Later Stone Age "Bushmen" and "Hottentots". The former were largely hunter-gatherers while the latter were mainly herdsman. Archeological studies are beginning to elucidate the rather complex way in which they shared and utilized the landscape. Domestic livestock (sheep) are known from the southern Cape from at least 17 000 B.P. (Schweitzer and Scott, 1973) and the proportions of bones in the most recent layers of some cave deposits suggest that the inhabitants were principally herders (Klein, 1977). Early travellers (Sparrman, 1785; Thunberg, 1796) indicate that primitive herders made judicious use of fire and were astute veld managers who moved their settlements as soon as veld conditions began to deteriorate. The scenario before the advent of the Europeans can be summarized briefly as follows: a localised but intense grazing by fairly low populations of domestic and indigenous ungulates ('pulse disturbance grazing' of Noble and Slatyer, 1980). Grazing was most likely concentrated on the more nutritive pastures on Bokkeveld shale, dune sands and some Enon beds (cf. Stinder *et al.*, 1965). Veld on T.M.G. quartzites would then, as now, have a lower cover of grasses which were predominantly 'sour' and supported a relatively low herbivore biomass. Fires were started both by man and other factors (lightning, rock falls) and the fire régime was probably variable.

A reconstruction of vegetation at the beginning of historic times can unfortunately only be inferred from the vague accounts of early travellers and also from present day vegetation relics. The course of the eastern migration of the 18th Century 'trekboers' proceeded through the Langkloof and into the Humansdorp region. As early as 1744 a 'loan' farm had been registered at the Kabeljous river near Jeffreys Bay and in 1770 the Gamtoos river was declared the eastern colonial boundary (Botha, 1923). Many travellers (Sparrman, 1785; Paterson, 1790; Thunberg, 1796; Lichtenstein, 1812; Campbell, 1815) commented favourably on the grassveld between the Kromme and Seekoie rivers. In Lichtenstein's (1812) words: "Large tracts of land near Gamtoos are covered with wholesome nourishing grass ... on which were grazing ... a great variety of wild animals, particularly oribi". Eland, quagga, zebra and hartebees were also noted in the surroundings (Paterson, 1790). Buffalo and elephant were observed in the valley thicket and hippo in the rivers (Sparrman, 1785; Paterson, 1790; Skead, 1980). From Seekoie river mouth travellers headed northwards across the Coastal Platform, towards the Gamtoos valley where the village of Hankey now stands. They would therefore have to traverse fynbos about which Steedman (1835) had this to say: "The surface of the plain consisted of a sandy gravelly soil, perfectly hard, with moor-like vegetation and scarcely a tree to enliven the dreariness of the route".

One of the first results of early settled agriculture was the elimination of the aboriginal graziers and indigenous ungulates, and the replacement of the latter with the settler's domestic livestock. Farms were large and uncamped and stocking rates initially low (Gerryts, 1949). There followed a period of light selective grazing. Gradually livestock numbers increased, farms were subdivided and stocking rates rose sharply. Veld was, and is, burnt as often as possible (four to five year cycle) in mid- to late summer (Smith, 1967). A combination of continuous overgrazing and the lack of post-fire rests, resulted in widespread veld deterioration (Smith, 1967; Liebenberg, 1945). These malpractices have persisted until recent times. In a survey of the Humansdorp region carried out by Smith (1967) 33% of the sample farms were not divided into grazing camps and only 14% of the farmers rested their veld for more than six months after a fire.

Major changes in vegetation are probably correlated with the transition from pulse- to continuous disturbance grazing régimes and from a patchy to a rigid and uniform fire régime. Today, the grasslands on the Bokkeveld shale and Enon conglomerate coastal flats have been largely replaced by renosterveld shrublands, although a few grassland relics remain. The spread and thickening up of Elytropappus rhinocerotis (renosterbos) in southern and south eastern Cape coastal grasslands has been well documented (Sparrman, 1785; Levyns, 1926; Hall, 1934; Bagshaw-Smith, 1937; Du Toit and Du Toit, 1938; Smit, 1943; Levyns, 1956). I propose a mechanism for the encroachment of grassland by E. rhinocerotis later in this paper (see also Cowling, 1982c).

Changes in fynbos vegetation have probably been less drastic, involving mainly the elimination of the fire-sensitive seed regenerating species (Cowling, 1982b). Undisturbed thicket is not fire-prone and its total extent is unlikely to have contracted much in historical times. The great fire of 1869, which raged uninterrupted from the south western Cape to Uitenhague, probably destroyed isolated pockets of thicket and forest in the study area (cf. Gerryts, 1949).

2.0 METHODS

2.1 Data collection

2.1.1 Sampling strategy

The two major physiographic units in the study area (coastal foreland, valley/mountains) each required a different sampling strategy. In the former region an investigation of community response to disturbances such as burning, bush-cutting and grazing formed a major part of the study. After initial reconnaissance, I entituted vegetation on the basis of geological substrate. As a result of consultations with the local extension officer of the Department of Agriculture and Fisheries I was able to choose, as study sites on each parent material, a number of farms which reflected a wide range of management practices. Each farm formed a major site where relevés were selectively placed in homogeneous vegetation stands (cf. Werger, 1974) with a known history of utilization. To ensure an even sampling spread I placed a number of relevés outside these major sites. This sampling approach is essentially similar to the approach used by the Zurich-Montpellier School (Westhoff and van der Maarel, 1973; Werger, 1974). Random sampling would have resulted in unnecessary replication and the possibility of an unrepresentative sample with an imperfectly known utilization history.

The disturbance régime in the Gamtoos River valley and Elandsberg mountains is considerably less intense than the coastal forelands. I used direct gradient analysis (Whittaker, 1967) to compare coenoclines (cf. Whittaker, 1973) in mature fynbos and non-fynbos vegetation along parallel elevational gradients (Cowling and Campbell, 1982b). On both coenoclines sample sites were stratified by elevation and relevés were randomly located on each major aspect (N, S, E and W) within the site. Further relevés were placed along the coenoclines to ensure a representative sample for classificatory purposes.

2.1.2 Sampling intensity and plot size

Sampling intensity is largely governed by the aims of a particular study and is usually delimited by logistic and time constraints. In this study, I was not concerned with obtaining an accurate classification at the level of the association (sensu Westhoff and Van der Maarel, 1973), but rather the delineation of communities which expressed and characterized the floristic variation and integrity of higher syntaxonomic units.

However, the degree of variation considered integratable into a meaningful expression

TABLE 1. - Information content of 100 m² (10 x 10 m) plot size determined from species-area extrapolations (1 ha = 100% info.)

Community	100 m ² no. species	inform.	10 000 m ² no. species	Linear regression
Grasslands ¹				
<u>Themeda-Stenotaphrum</u>	41	38,8	105,8	Y = 7,35 + 24,6 log A r = ,93
<u>Thamnochortus-Tristachya</u>	52	58,4	89,0	Y = 21,4 + 16,9 log A r = ,99
<u>Themeda-Cliffortia</u>	42	55,7	75,4	Y = 10,0 + 16,4 log A r = ,97
<u>Elytropappus-Eustachys</u>	77	62,2	123,8	Y = 21,5 + 25,6 log A r = ,99
Small-leaved (Proteoid)				
Shrublands				
<u>Restio-Agathosma</u>	42	57,5	73,1	Y = 14,7 + 14,6 log A r = ,99
<u>Restio-Maytenus</u>	28	42,6	65,7	Y = 2,3 + 15,8 log A r = ,92
<u>Erica-Trachypogon</u>	32	46,1	69,4	Y = 10,2 + 14,8 log A r = ,96
<u>Erica-Trachypogon</u>	56	55,0	102,3	Y = 15,8 + 21,6 log A r = 1,00
<u>Erica-Thamnochortus</u>	35	64,0	54,7	Y = 15,7 + 9,7 log A r = 1,00
<u>Protea-Clutia</u>	68	62,6	108,7	Y = 26,4 + 20,6 log A r = 1,00
<u>Thamnus-Tetraria</u>	31	60,7	51,1	Y = 13,3 + 9,5 log A r = 1,00
<u>Themeda-Cliffortia</u>	58	63,3	91,7	Y = 23,6 + 17,0 log A r = 1,00
<u>Elytropappus-Eustachys</u>	69	62,3	110,8	Y = 23,6 + 21,8 log A r = ,99
<u>Elytropappus-Relhania</u>	65	57,4	113,2	Y = 12,7 + 25,1 log A r = ,99
Large-leaved (Succulent)				
Shrubland (Thicket)				
<u>Pterocelastrus-Euclea</u>	39	58,5	66,7	Y = 10,3 + 14,1 log A r = 1,00
<u>Pterocelastrus-Euclea</u>	54	47,9	112,7	Y = 10,1 + 25,6 log A r = ,98
<u>Pterocelastrus-Gonioma</u>	48	54,8	87,6	Y = 14,4 + 18,3 log A r = 1,00
<u>Euclea-Brachylaena</u>	57	45,9	124,3	Y = 4,0 + 30,1 log A r = ,99
<u>Sideroxylon-Euphorbia</u>	37	50,8	72,8	Y = 10,9 + 15,5 log A r = ,98
Forest				
<u>Rapanea-Canthium</u>	35	50,0	75,0	Y = 7,6 + 16,9 log A r = ,99

¹ Structural characterization here and elsewhere in this paper according to Campbell et al. (1981).

of a vegetation unit is still a matter of judgment (Mueller-Dombois and Ellenberg, 1974). I sampled a total of 194 relevés, including 879 species. After the classifications were constructed I located 51 "test" plots in undersampled areas. With a few exceptions it was possible to integrate these plots into the established communities.

Werger (1972) defines optimal plot size as that size nearest to the minimal area, giving the best compromise between information obtained and effort expended. Much research has been aimed at clarifying the concept of minimal area but it appears that an objective definition is impossible (Werger, 1972; Kershaw, 1973). In this study it was necessary to have a fixed plot size to facilitate comparisons of species richness (see Cowling, 1982f). I used the approach of Werger (1972) which determines the optimal plot size as having a 50–55% content of a hectare information (number of species in a hectare). Using the standard species–area relationship and regarding one hectare as having an information content of 100%, optimal plot size can then be determined on the basis of the resolution desired for the study.

Nested quadrats containing plot sizes 1, 5, 10, 100 and 1 000 m² (see Whittaker *et al.*, 1979) were sampled in a wide range of vegetation types in the study area. With a few exceptions, 10 x 10 m plots retrieved the desired level of information (>50%) (Table 1) and this size was considered optimal for all vegetation in the study area. Two of the communities on coastal dunes (Themeda–Stenotaphrum and Restio–Maytenus), apparently required larger plots. Here communities form a complex mosaic of successional states and it is often difficult to locate homogeneous stands of 1 000 m².

A plot size of 10 x 10 m has been used in fynbos and Afromontane forest in the south western Cape (Werger *et al.*, 1972; McKenzie *et al.*, 1977; McKenzie, 1978) but most fynbos studies use smaller plots (5 x 10 m) (e.g. Taylor, 1969; Bond, 1981).

2.1.3 Vegetation parameters and site variables

Within each relevé I subjectively estimated percentage projected canopy cover of each species. Species were classed into growth forms and additional structural data were recorded (for details see Cowling and Moll, 1982). Nomenclature follows the Albany Museum Herbarium (B.R.I.) in Grahamstown, where species were identified. Environmental variables recorded in the relevés are shown in Table 2.

TABLE 2. - Environmental variables recorded in all relevés. Soil chemical data for the A horizon only from a subset of 97 samples.
Some details on methods and classes of variables are shown

VEGETATION AGE	Post-fire, post bushcut. Estimates in years based on information from landowners.
ANNUAL RAINFALL	1 : 250 000 isohyet maps and local weather stations.
ALTITUDE	1 : 50 000 topographic sheets.
ASPECT	Classes : 1 = SE, 2 = S, 3 = SW, 4 = E, 5 = W, 6 = NE, 7 = N, 8 = NW: a cool to hot gradient estimated from aspect-radiation flux data (cf. Schulze, 1975).
SLOPE INCLINATION	
LITTER COVER (%)	
GRAZING INTENSITY	Classes: ungrazed = 1; light = 2; moderate = 3, heavy = 4; overgrazed = 5. Scale based on current stocking rate, past grazing and the effects of grazing (cf. Roberts and Opperman, 1974; Roberts <u>et al.</u> , 1975).
GEOLOGY	Sheets 151 north and south, Gamtoos river (Haughton <u>et al.</u> , 1937).
ROCK COVER (%)	
SOIL DEPTH	
SOIL FORM	MacVicar <u>et al.</u> (1977)
SOIL TEXTURE	Estimated for all relevés and tested using results of a textural analysis (pipette method) of samples from 97 relevés (textural classes according to MacVicar <u>et al.</u> , 1977).
% SAND CONTENT	Pipette method.
pH	1 N KCl 1:2,5 soln.
EXCHANGEABLE CALCIUM)) 1 N NH ₄ acetate leachate
S VALUE	Sum of exchangeable cations)
OXIDIZABLE CARBON	Walkley-Black method .
TOTAL NITROGEN	Kjeldhal.
AVAILABLE PHOSPHORUS	Bray No. 2 (acid extraction, pH 3) Modified Olsen (alkali extraction, pH 8)

2.2 Data analysis

2.2.1 Community classification

On the coastal plain I initially entitaded vegetation according to geological substrate because parent material appeared to be a major factor in determining the distribution of vegetation types (cf. Taylor, 1978; Kruger, 1979; Boucher and Moll, 1980). This assumption was largely corroborated by the results of a polythetic agglomerative classification of the whole data set (group-average sorting using relativized Czekanowski coefficient (Campbell, 1978)). An identical classification of the relevés from the Gamtoos/Elandsberg region showed that this data set could be divided into two groups - fynbos/renosterveld and thicket/forest communities.

I used two-way indicator species analysis (TWINSpan; Hill, 1979) to classify relevés of each data set. TWINSpan is a recent improvement on indicator species analysis (ISA: Hill *et al.*, 1975). ISA is a polythetic, divisive classificatory technique which has proved successful in a variety of vegetation types (Hill *et al.*, 1975; Hall and Swaine, 1976; Basset, 1978; Daniels, 1978). TWINSpan and ISA produce a classification of stands by the progressive splitting of ordinations (reciprocal averaging; Hill, 1973) at their centres of gravity. At each split indicator (diagnostic) species are chosen to define the two groups of data; serious misclassifications are rare (Hill, 1979). TWINSpan produces a classification of species as well as stands and is designed to construct an ordered two-way table which approximates the tabular matrix arrangement of the Zurich-Montpellier School and, as such, is a highly promising technique (Gauch and Whittaker, 1981). TWINSpan therefore approaches the much desired integration of classical syntaxonomy with numerical phytosociology (cf. Dale and Webb, 1975; Komarkova, 1980). The technique has been used successfully in southern Cape fynbos communities by Bond (1981).

I compared the two-way phytosociological tables produced in the classifications and extracted synoptic tables for each order (see below). These tables (Tables 4 to 10) summarise species fidelity to communities within an order and the diagnostic value of species of that order. Fidelity is rated on a 1 - 5 scale: 1 = 1 - 20% frequency; 2 = 21 - 40%; 3 = 41 - 60%; 4 = 61 - 80%; 5 = ≥ 81%. Only those species with values greater than 1 in one or more communities were included in the synoptic tables.

I determined diagnostic values for species in relation to orders. Species marked * are diagnostic for a particular order and include both character and differential species (cf. Werger, 1974); species marked ¹ are also diagnostic species but are regional and

local endemics and are either local or general character taxa (cf. Werger and Van Gils, 1976). A more detailed analysis of species diagnostic values must await more extensive phytosociological studies in the southern and eastern Cape.

2.2.2 Syntaxonomic ranking

At present there are inadequate plant community data in the Fynbos Biome to facilitate a rigorous and formalized syntaxonomic treatment. The ranks I propose here are tentative and are not formally defined in terms of quantitative measures of plot similarity. The hierarchical system I present (Table 3) is an attempt to meet the guidelines proposed by the Botanical Research Institute (n.d.).

In this study sampling was not sufficiently intense to extract associations (sensu Werger, 1974) as the final syntaxonomic unit. I have termed the ultimate units "communities"; in some cases they are equivalent to associations but could mostly be ranked as alliances. The pivotal rank in this treatment is the order (orders are mapped in Fig. 3). Following Van der Muelen's (1979) treatment of western Transvaal bushveld, I regard the order as being roughly equivalent to an Acocks (1953) veld type. It is an agro-ecological unit comprising a range of communities which are biogeographically and structurally related and have broadly similar habitat requirements. The order is a useful mapping unit as a first stage in planning and development. I have called the highest unit a class which comprises a group of related orders.

These definitions are unfortunately vague and clearly do not correspond to the more explicitly stated definitions in classical phytosociology. A clearer picture of the ranks emerges in later discussions. In the Cape fynbos communities where gamma and delta diversity is very high (Kruger and Taylor, 1979) there are likely to be large numbers of syntaxa of all ranks. Many orders will have the same agro-economic potential since, particularly in the western Cape, composition may change drastically with very little change in environment.

2.2.3 Community nomenclature

Varied approaches to the classification of the plant communities in South Africa have resulted in a chaos of syntaxonomic nomenclature. Recently the Botanical Research Institute (n.d.) has proposed a series of guidelines, based largely on the code laid down by Barkman *et al.* (1976), for a standardized system of syntaxonomic nomenclature for South Africa. I have used these guidelines in the community nomenclature presented below (see Tables 4 – 10).

The nomenclature includes a binomial specific connotation where the first species is a dominant and the second that of a differential or character species. This is followed by a locality-structural term, e.g. Humansdorp Grassy Fynbos. At least one of the species names of the binomial (preferably the first, dominant one) is a species whose presence and abundance is not grossly affected by the currently applied fire and grazing régimes. Each community is given a formal structural description according to the system of Campbell *et al.* (1981) (Cowling, 1982 a-d).

2.2.4 Biogeographical analysis

I determined the phytochorological affinities of each species in terms of established phytochoria (Werger, 1978; White, 1982). The distribution of taxa were established from locality records in the Albany Museum Herbarium (GRA) and the Bolus Herbarium (BOL) and from distribution maps in recent revisions. Species were classified as:

- (i) endemic to a particular phytochorion;
- (ii) linking two (usually) adjacent phytochoria;
- (iii) widely distributed, common in tropical and subtropical phytochoria;
- (iv) widely distributed, occurring in temperate and tropical phytochoria and often extending outside Africa.

Categories (ii) – (iv) are ecological and chorological transgressor species of White (1971).

Regional and local endemics were classed as being of Cape, Afromontane, karroid (Karoo-Namib) or subtropical (chiefly Tongaland-Pondoland) affinity. Cape endemics are restricted to Weimarcks (1941) South-Eastern Centre. Karroid and subtropical endemics are restricted to the Kaffrarian Transition Zone (Cowling, 1982e), a region extending from the Humansdorp district eastwards to the Kei river and bounded in the north by the Sneeuwberg-Winterberg axis. I give details and examples of distribution patterns elsewhere (Cowling, 1982e).

2.3 Community dynamics

An understanding of community dynamics is essential for the full characterization of vegetation subjected to recurrent disturbances. In managed natural systems a knowledge of dynamics provides the soundest basis for long term management (Slatyer, 1976).

I studied the dynamics of fynbos and renosterveld communities of the coastal forelands and the results are fully discussed in Cowling (1982, a-c). As these results are referred to in this paper, I undertake below to outline the approach and methods used to study dynamics and to clarify the assumptions implicit in these methods.

In South Africa, the study of vegetation dynamics, particularly secondary succession, has been severely limited by the Clementsian dynamics paradigm (e.g. Phillips, 1931; Acocks, 1953 and many others). The classical view of ecological succession and the climax (Clements, 1916) is that, following a disturbance there is a community replacement sequence which culminates in the final community (climax) which is in equilibrium with the prevailing environment. Implicit in this view is the assumption that each assemblage of species (community) modifies the site conditions so that it becomes less suitable for its own persistence and more suitable for its successor. Furthermore, Clements assumed that, given time, a climax vegetation of the same general type (monoclimax) will be produced and stabilized in a similar climatic region, irrespective of earlier site differences. These concepts are still upheld in the literature (e.g. Odum, 1969).

Clements' concepts have proved to be unrealistic and unworkable in the field and attempts to uphold them have resulted in a confusion of terms to accommodate situations which do not fit the ideal. Two papers have effectively undermined the assumptions of Clementsian ecology. Whittaker's (1953) incisive and exhaustive paper on climax concepts liberated botanists from the monoclimax paradigm in a manner more realistic than Tansley's (1935) earlier attempt. The essence of Whittaker's analysis is as follows: "There is no absolute climax for any area, and climax composition has meaning only relative to position along environmental gradients . . . All climaxes are edaphic as well as topographic and climatic climaxes . . . All are part of the climax pattern". Drury and Nisbet (1973) present a devastating criticism of the generalizations made by classical succession theory. They refute the universality of the classical "relay floristics" model of succession (see also Egler, 1954) and stress the importance of initial floristic composition of the site in determining successional pathways. They also note that modification of the environment by plants acts generally to delay succession and not facilitate the invasion of the site by new species.

The reviews cited above and later papers (e.g. Horn, 1974; Pickett, 1976; Connel and Slatyer, 1977; Van Hulst, 1978; Noble and Slatyer, 1980; Glenn-Lewin, 1980; Peet and Christensen, 1980) have emphasized life history properties (colonizing ability, dispersal, growth rates, longevity) of individual species (cf. Gleason, 1926) and not the emergent properties of communities, in determining the pattern of succession. Two useful developments are Connel and Slatyer's (1977) description of successional pathways in terms of species facilitation, tolerance and inhibitive properties, and Noble and Slatyer's (1980) use of species' vital attributes to predict post-disturbance successional pathways.

Methods to study community dynamics range from inductive studies (observations and experiments) to deductive studies using both simple qualitative and complex quantitative models (Goodall, 1977). For philosophical and practical reasons, the deductive approach is preferred, although long-term observations will always be required to validate predictions.

The approach I used was to select sites of known disturbance history, encompassing a wide range of disturbance features (see 2.1 above). I used TWINSpan (see 2.4.1 above) to classify relevés in terms of floristic and structural attributes (Cowling, 1982 a-c; Cowling and Moll, 1982). In this way samples were organised into a manageable number of floristic and structural community-types which were then subjected to further investigation (cf. Slatyer, 1976; Austin, 1977). A comparison of the two classifications showed that within each floristic community there were a number (usually two) of structural communities or structural "cover states" which I assumed corresponded to different successional developments of that community. The assumption that spatially separate vegetation represents states of the same system at different stages of development has been criticized recently (Drury and Nisbett, 1973; Goodall, 1977). In my study this assumption is supported by the high floristic similarity of diverse structural types and the existence of fenceline contrasts (Figures 30, 32) where the disturbance régime was the only site variable that differed across the fenceline.

I used the qualitative model employing vital attributes of species (Noble and Slatyer, 1980) to predict successional patterns under different disturbance régimes. These predictions were tested against vegetation samples, of known disturbance history, that were collected for the multivariate analyses.

TABLE 3. - Syntaxonomic and synecological relationships of higher vegetation units in the Humansdorp region

Rank	Name	Structural characterization ¹	Distribution	Physiography (in Fynbos Biome)	Rainfall ² (mm yr ⁻¹)	Soil
Class	Cape Fynbos Shrublands	Variable: mainly Proteoid Shrubland, Heathland, Small-leaved Shrubland, Restioid	SW, S and SE Cape	Mountains and coastal forelands (coastal sands and calcrete) of the Cape Fold Belt	250 - 3 300	Variable (see below)
Order	South Eastern Mountain Fynbos	Tall Mid-dense Proteoid Shrubland, Closed Restioid, Low Closed Heathland	Eastern Baviaanskloof and Kouga, Elandsberg, Van Stadens and Groot Winterhoek Ranges	Upper south slopes in drier western regions; from near sea level on pediments in the east (Van Stadensberg)	>750	Acid, infertile, shallow to deep sandy loams; apedal subsoils often with an eluviated horizon, drainage variable
Order	Grassy Fynbos	Mid-high, mid-dense Grassy Proteoid Shrubland, Low Mid-dense Grassy Heathland, Low Mid-dense Grassy Small-leaved Shrubland, Restioid Grassland	Baviaanskloof, eastern Kouga, Zuuransberg, Elandsberg, Van Stadensberg, Groot Winterhoek, Groot River Heights and Zuurberg ranges; Tsitsikamma, Humansdorp and Albany Coastal Forelands	North and lower south slopes of ranges; Tertiary planation surfaces and coastal forelands; mainly south slopes in the Zuurberg	400 - 750	Acid, infertile shallow to deep sandy loams to loamy sands; often of colluvial origin; some paleosols on coastal forelands; drainage variable
Order	South Coast Dune Fynbos	Low Mid-dense, Small-leaved Shrubland/ Low Open Large-leaved Shrubland, Closed Restioid Grassland	Cape Flats to Cape Recife, along the coast	Coastal dunes	300 - 800	Mostly deep, neutral to alkaline calcareous sands; occasionally lithosols on calcrete; drainage variable
Class	Cape Transitional Small-leaved Shrublands	Open (Mid-dense) Small-leaved Shrubland	SW, S and SE Cape; possible outliers on the Great Escarpment of the south central Cape	Coastal forelands and intermontane valleys, pediments and lower (mostly north) slopes of Fold Mountains in drier regions	300 - 600	Highly variable: duplex soils on coastal forelands and intermontane valleys; colluvial soils and lithosols on lower mountain slopes; more fertile and often heavier in texture than fynbos soils
Order	South Coast Renosterveld ³	Mid-dense Grassy Small-leaved Shrubland, Closed (Mid-dense) Grassland	Caledon to Uitenhage with outliers near Grahamstown	Coastal forelands and intermontane valleys of the coastal ranges	300 - 600	Shallow to deep neutral to slightly acid soils with clayey, usually structured sub-soils; often base saturated; poorly drained with seasonally high watertable in subhumid regions

¹ Structural characterization according to Campbell et al. (1981).² Rainfall limits are approximate and do not take into account local variations of slope, soil drainage and texture, all of which affect soil moisture.³ The term "Renosterveld" (Boucher, 1980) is used instead of Rhenosterbosveld (cf. Acocks, 1953).

Rank	Name	Structural Characterization ¹	Distribution	Physiography (in Fynbos Biome)	Rainfall ² (mm yr ⁻¹)	Soil
Class	Subtropical Transitional Thicket	Closed (Mid-dense) Large-leaved (Succulent) Shrubland	Kei to Gouritz rivers with outliers in river and intermontane valleys and coastal forelands in the SW Cape	Interfluvies (termitaria), river valleys and coastal dune sands of the coastal forelands; intermontane valleys and lower mountain slopes (screes)	300 - 750	Mostly deep neutral to slightly acid clayey soils; also deep calcareous coastal dune sands and colluvial soils (screes) on lower mountain slopes; moderately fertile; always well drained
Order	Kaffrarian Thicket	Tall Closed Large-leaved (Semi-succulent) Shrubland	As above	As above	500 - 750	As above
Order	Kaffrarian Succulent Thicket	Tall (Mid-high) Closed (Mid-dense) Large-leaved and Succulent Shrubland	Kei to Gouritz river valleys	Mainly river valleys (Kei, Fish, Sundays, Gamtoos, Gouritz) with outliers in intermontane valleys of the inland Fold Mountains (Kouga, Baviaanskloof, Swartberg)	350 - 500	Mostly deep, moderately fertile and well-drained bottom-land soils
Class	Afromontane Forest	Tall (Low) Forest	SW Cape to NE and W Africa; always at high altitudes in tropical and subtropical Africa; 0-1 500 m in S and SW Cape, 600-1 500 m in E Cape, 900-2 150 m in Natal, above 1 500 m in the Transvaal	On the coastal ranges of the Cape Folded Belt but also on coastal forelands (Knysna region); always in sheltered sites having adequate soil moisture throughout the year	> 800 (S and SW Cape)	Acid, mostly deep organic-rich soils of good moisture status
Order	Knysna Afromontane Forest	As above	Uitenhage to the Cape Peninsula	As above	As above	As above

¹ Structural characterization according to Campbell *et al.* (1981).

² Rainfall limits are approximate and do not take into account local variations of slope, aspect, soil drainage and texture, all of which affect soil moisture

³ The term "Renosterveld" (Boucher, 1980) is used instead of Rhenosterbosveld (cf. Acocks, 1953).

3.0 THE SYNTAXA

In this section I define and give terms to the syntaxonomic concepts. Data summarizing structural and ecological relationships of the classes and orders are shown in Table 3. Tables 4 - 10 summarize floristic data. Figures 9 and 35 show phytochorological spectra and patterns of endemism, and Figures 10 and 36 show some structural data, for selected communities.

3.1 Cape Fynbos Shrublands

I use the term "Cape Fynbos Shrublands" to describe a class of communities that includes the fynbos vegetation of the Cape Floristic Region. Specht (1979) and Specht and Moll (1982) include Cape fynbos within a global heathland concept. However not all Cape Fynbos Shrublands are heathlands sensu Specht (1979). In accordance with the structural scheme proposed by Campbell et al. (1981) I restrict the use of the term heathland to those communities having a high cover of true heaths (Ericales) (see also Bond, 1981; Campbell, 1982b). Therefore the more general term "shrubland" which includes heathlands, is preferred.

A precise definition and delimitation of Cape fynbos vegetation eludes botanists up to the present. In a recent review of the Cape phytogeographical region Taylor (1978) defined fynbos as follows: "Floristically fynbos can be defined by . . . the lack of single species dominance and/or the conspicuous presence of members of the family Restionaceae. Physiognomically fynbos is characterized by three elements, restioid, ericoid and proteoid". Kruger (1979), in another review, accepts Taylor's definition and states that ". . . the only constant and differential floristic element is the Restionaceae". Both authors give a list of typical genera.

These definitions are easily confuted. A general lack of single species dominance in fynbos is a myth: fynbos communities often have dominance concentrated in one or two species (Cowling, 1982f). Restionaceae are prominent in the Southern Variation of the Strandveld (34a) (Acocks, 1953; Boucher and Jarman, 1977) and occasional in Coastal Renosterbosveld (46) (Acocks, 1953; Boucher, 1982; Cowling, 1982c), both non-fynbos types. Afromontane fynbos (Killick, 1979), although often lacking Restionaceae, has a similar structure and generic composition to Cape fynbos (see Story, 1952; Phipps and Goodier, 1962; Killick, 1963; Edwards, 1967; Van der Schijff and Schoonraad, 1971). In these communities typical fynbos genera as defined by Taylor (1978) and Kruger (1979-)

include Protea, Erica, Muraltia, Cliffortia, Passerina, Phylica, Metalasia, Stoebe, Helichrysum, Merxmüllera and Pentaschistis. Some workers regard the Cape as an extension of the Afromontane region (Adamson, 1948; Tinley, 1975; Linder, 1982).

I define the class Cape Fynbos Shrubland in terms of biogeographic, structural and ecological criteria as follows:

- (i) Sample floras show a phytochorological spectrum in which approximately 50% of the species are restricted to the Cape phytochorion as delimited by Werger (1978). The majority of the remaining species are largely Cape linking taxa (Fig. 9).
- (ii) A high incidence of regional endemism (cf. Weimarck, 1941). Regional endemics are mostly of Cape affinity. Some data are available for the study area (Fig. 9) but more are needed for a quantitative assessment.
- (iii) Structural definition according to Campbell (1982b) reflecting characteristics of the "heathland syndrome" (small leaves, proteoid isobilateral leaves, sclerophylly, evergreen hemicryptophytes (cyperoids and restioids) (Specht, 1979; Fig. 10)). Campbell's (1982b) structural definition of fynbos of the Cape Fold Mountains and my biogeographic definition show good agreement in the study area.
- (iv) Ecologically restricted to areas receiving a substantial proportion of winter rainfall and having sandy, infertile soils and alkaline calcareous sands (Table 3).

Due to the high gamma diversity of Cape fynbos (Kruger and Taylor, 1979) future phytosociological studies will most certainly result in a proliferation of phytocoenoses at all syntaxonomic ranks. A structural treatment of fynbos (Linder and Campbell, 1979; Bond, 1981; Campbell, 1982b) is probably more pragmatic at this stage.

I recognised three Cape Fynbos Shrubland orders in the study area.

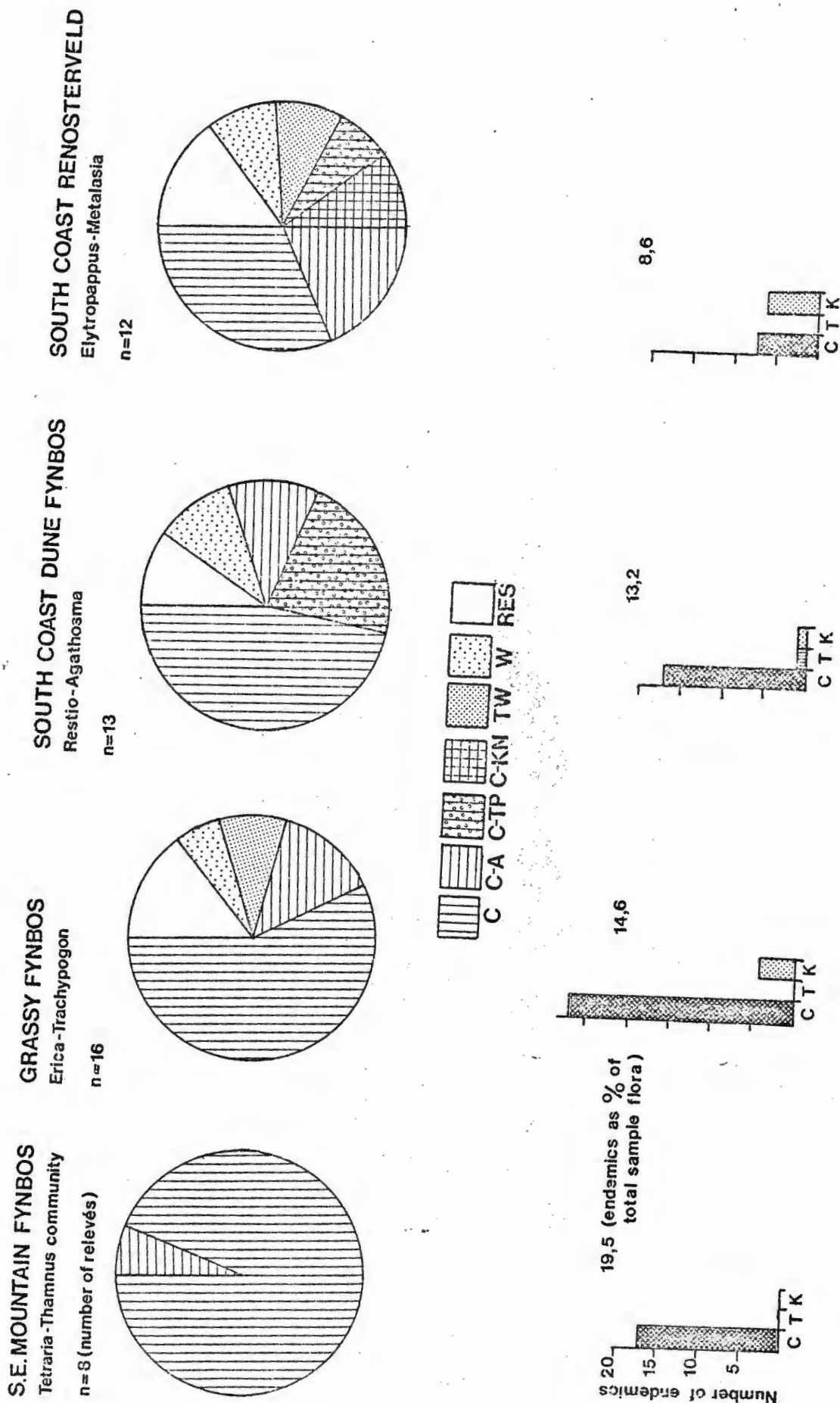


Fig. 9. Phytochorological spectra and endemism for Cape Fynbos Shrublands and Cape Transitional Small-leaved Shrublands (Elytropappus-Metatalasia community). C = Cape endemics; C-A = Cape-Afromontane linking species; C-TP = Cape-Tongaland-Pondoland linking species; C-KN = Cape-Karoo-Namib linking species; subtropical wides; W = wides; RES = residual (groups contributing less than 5% total species); TW = Tropical-Geographical affinity of endemics: C = Cape; T = Subtropical; K = Karroid.

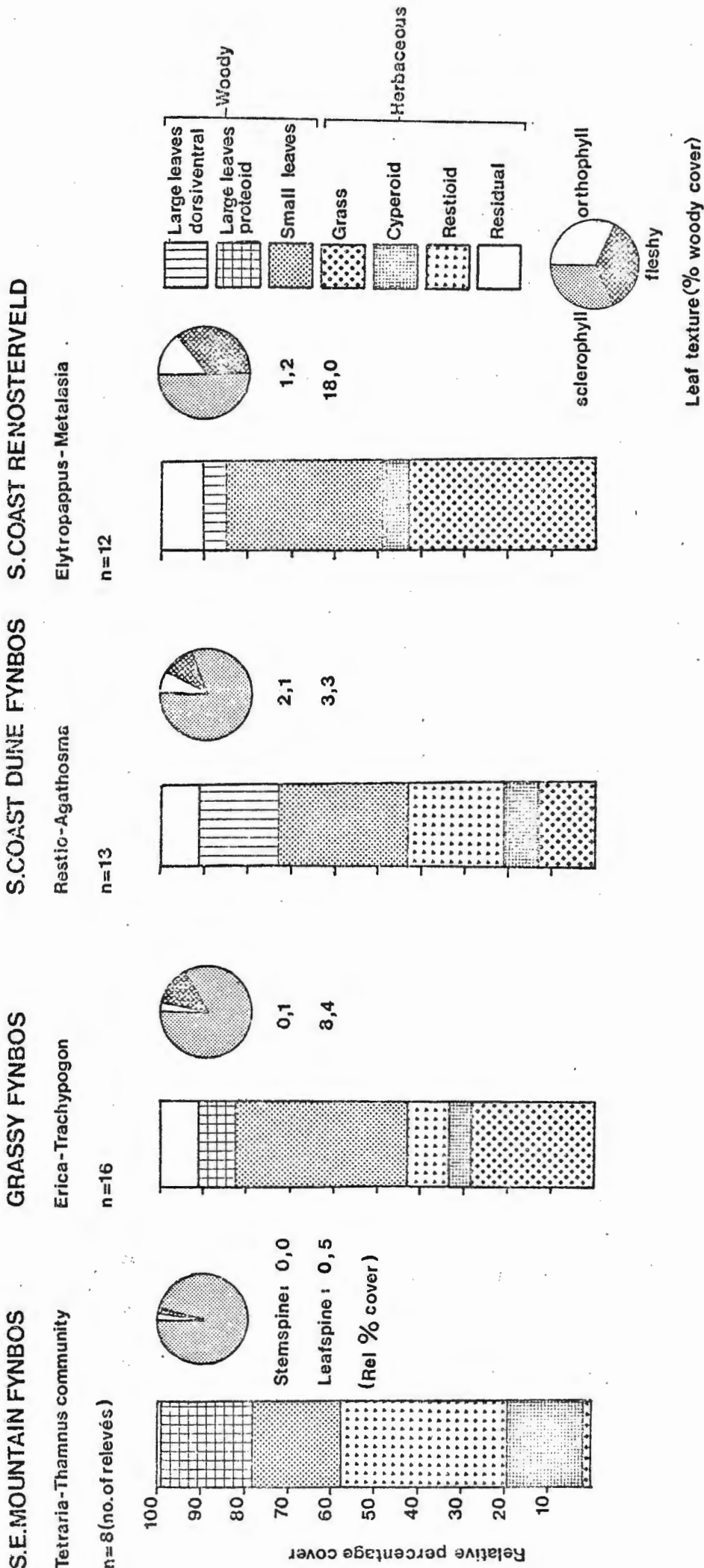


Fig. 10. Growth form composition of Cape Fynbos Shrublands and Cape Transitional Small-leaved Shrublands (*Elytropappus-Metalasia* community). Definition of growth forms as in Campbell et al. (1981). Leaf texture categories defined in Cowling and Campbell (1982a).

3.1.1 South Eastern Mountain Fynbos

Mountain Fynbos is the term used by Taylor (1978) and Kruger (1979) to replace Acocks' (1953) *Macchia* (69) and *False Macchia* (70). The term is an unfortunate choice since Mountain Fynbos communities are frequently found near the coast (cf. Coastal Fynbos). However, the term is well entrenched in the literature and there is little point in discarding it.

Mountain Fynbos comprises communities of the Cape Folded Belt from the Cedarberg in the northwest to the Groot Winterhoek mountains in the southeast. It occurs under a sub-humid to humid rainfall régime in the western and southern Cape ($>400 \text{ mm yr}^{-1}$) and in moist upland regions ($>750 \text{ mm yr}^{-1}$) in the south eastern Cape. Mountain Fynbos is invariably restricted to acid infertile and sandy soils derived from quartzites and sandstones of the T.M.G. Communities are almost entirely composed of Cape endemics and regional endemism is high (Fig. 9). Grasses are rare and when present, are of the C_3 type (e.g. *Pentaschistis*, *Merxmüllera*); large-leaved dorsiventral shrubs and other subtropical growth forms are lacking (Fig. 10). Structurally the communities are Mid-dense to Closed Shrublands, Heathlands and Restiolands. Mountain Fynbos communities have been described by Taylor (1969), Werger *et al.* (1972), Boucher (1978), McKenzie *et al.* (1978), Glyphis *et al.* (1978), Laidler *et al.* (1978), Bond (1981), Taylor and Van der Meulen (1981).

South Eastern Mountain Fynbos occurs in the eastern Baviaanskloof and Kouga mountains and the Groot Winterhoek and Elandsberg ranges (pers. obs.) (see Table 3). Mountain Fynbos in the study area was undersampled and I recognised only two communities; floristic data are shown in Table 4.

The *Tetraria-Thamnus* community occurs in humid ($800 - 1\,000 \text{ mm yr}^{-1}$) upper ($>400 \text{ m}$) regions of the eastern Elandsberg range (Fig. 11). Soils are shallow leached, acid and infertile loamy sands (Fig. 8) of the Mispah, Glenrosa, Cartref and occasionally Oakleaf forms. On the drier lower slopes is the *Leucospermum-Tetraria* community which is transitional to Grassy Fynbos (see below). Soils are mainly Glenrosa and Mispah. Community dynamics were not studied. More details on these communities and their environmental relationships are given in Cowling (1982d).

TABLE 4. - South Eastern Mountain Fynbos communities

Community	A	B
Number of relevés	8	5
* <u>Tetraria capillacea</u>	5	
¹ <u>Thamnus multiflorus</u>	5	1
* <u>Tetraria involucrata</u>	4	
* <u>Pentaea cneorum</u>	4	
* <u>Erica copiosa</u>	4	
¹ <u>Helichrysum felinum</u>	4	1
<u>Leucadendron laurifolium</u>	3	
¹ <u>Hypodiscus synchronolepis</u>	3	
<u>Agathosma pilifera</u>	3	1
* <u>Protea eximia</u>	3	1
¹ <u>Agathosma venusta</u>	2	
* <u>Protea mundii</u>	2	
* <u>Cyclopia subternata</u>	2	
<u>Cannomois virgata</u>	2	
<u>Erica pectinifolia</u>		5
<u>Ficinia gracilis</u>		4
<u>Anthospermum ciliare</u>	1	4
<u>Tetraria compressa</u>	2	5
<u>Leucospermum cuneiforme</u>	2	4
<u>Protea neriifolia</u>	2	4
<u>Diheteropogon filifolius</u>	1	4
* <u>Brunia nodiflora</u>	2	4
<u>Restio fruticosus</u>		3
<u>Trachypogon spicatus</u>		3
<u>Muraltia squarrosa</u>		3
<u>Themeda triandra</u>		2
<u>Leucadendron salignum</u>		2
<u>Erica demissa</u>		2
<u>Eragrostis capensis</u>		2
<u>Restio triticeus</u>	4	5
<u>Tetraria cuspidata</u>	4	5
<u>Hypodiscus striatus</u>	4	5
* <u>Hypodiscus albo-aristatus</u>	4	5
<u>Centella virgata</u>	4	5
* <u>Leucadendron eucalyptifolium</u>	4	3
<u>Disparago ericoides</u>	4	3
<u>Gnidia coriacea</u>	3	2
* <u>Osteospermum junceum</u>	2	2
<u>Indigofera sulcata</u>	2	2
<u>Aspalathus rubens</u>	2	2

A : Tetraria capillacea-Thamnus multiflorus Elandsberg Proteoid Mountain Fynbos

B : Leucospermum cuneiforme-Tetraria compressa Elandsberg Dry Proteoid Mountain Fynbos

* Diagnostic species for South Eastern Mountain Fynbos, including:

¹ South Eastern endemics (Weimarck, 1941) largely restricted to S.E. Mountain Fynbos



Fig. 11: Mature S.E. Mountain Fynbos, Tetraria-Thamnus proteoid community on shallow leached loamy sand (Cartref form) in the Elandsberg Mountains (c. 500 m). Dominant species: Leucadendron loerinse, Hypodiscus striatus, H. synchroolepis, Erica copiosa. Between Loerie and Otterford forest stations.



Fig. 12: Erica-Trachypogon Grassy Fynbos on colluvial gravels north of Humansdorp. Kaffrarian Thicket on termitarium. Fynbos species include Phylica abutina, Erica pectinifolia, Leucadendron salignum, Trachypogon spicatus, Restio triticeus, Themeda triandra, Merxmuellera stricta and Bobartia orientalis. Near Misgund (c. 220 m).

3.1.2 Grassy Fynbos

The concept of Grassy Fynbos presented here is new. It includes the fynbos communities of the lower and north slopes and planed forelands of the Cape Folded Belt in the south eastern Cape (Table 3). Both Taylor (1978) and Kruger (1979) mention the increased grassiness of the south eastern Cape fynbos but include it with Mountain Fynbos.

3.1.2a Characterization

Biogeographically Grassy Fynbos is characterized by a high proportion of Cape-Afromontane linking species and widely distributed tropical C4 grasses (Themeda, Trachypogon, Heteropogon, Brachiaria, Eragrostis) (Fig. 9). The order has good diagnostic species including a number of regional and local character taxa (Table 5). Structurally, Grassy Fynbos communities are similar to Mountain Fynbos except for the prominence of grasses in the understorey at the expense of restioids (Fig. 10). Soils are marginally more fertile than Mountain Fynbos soils (Fig. 8).

3.1.2b Grassy Fynbos as a false fynbos

The grassiness and Afromontane links of these communities probably led Acocks (1953) to his conjecture that they are derived from grassland and forest similar to the Afromontane communities of the eastern Cape (Dohne Sourveld, 41). This is Acocks' (1953) False Macchia concept which is clearly untenable for southern and south eastern Cape Mountain Fynbos where tropical grasses are absent. I argue below that the notion of Grassy Fynbos as a recently derived vegetation type is also untenable.

Evidence refuting Acocks' hypothesis is the large number of regional and local endemics of fynbos affinity in Grassy Fynbos. (Fig.9; Martin, 1966; Cowling, 1982e). Acocks (1979) recognized this as a fundamental flaw in his theory: he therefore introduced fynbos as a permanent feature of the landscape by invoking a "rotating climax" according to the Clementsian replacement sequence : scrub forest (thicket) → (fire) → grassland → fynbos → thicket. My observations in the study area and elsewhere provide little support for this hypothesis. The distribution of thicket in Grassy Fynbos is determined largely by the availability of special edaphic sites (deep water retaining soils of talus slopes, slope breccias and termitaria) (Fig. 12) (see also Martin, 1965). Some of the sites are fire-protected which probably facilitated the initial establishment of thicket seedlings. However, most Grassy Fynbos soils are shallow and stony or poorly drained

TABLE 5. - Grassy Fynbos communities

Community Number of relevés	A 14	B 16	C 9	D 5	E 7	Community Number of relevés	A 14	B 16	C 9	D 5	E 7
¹ <i>Passerina pendula</i>	5	1				<i>Helichrysum cymosum</i> ssp. <i>cymosum</i>	1	3	2	1	
<i>Restio cuspidatus</i>	4	1				<i>Agathosma capensis</i>	2	1	1		
* <i>Erica decipiens</i>	3					<i>Leucodendron salignum</i>	2	4	5	5	
<i>Chrysocoma tenuifolia</i>	3	1				<i>Helichrysum teretifolium</i>	3	2	5	5	1
<i>Euclea natalensis</i>	3					<i>Anthospermum ciliare</i>	4	4	3	5	
¹ <i>Phyllica abutina</i>	3	1				<i>Tetraria cuspidata</i>	3	5	5	3	
<i>Aspalathus rubens</i>		4	2			<i>Phyllica axillaris</i>	3	3	2	3	1
* <i>Chaetacanthus setiger</i>		3		1		<i>Disparago ericoides</i>	2	4	3	4	1
<i>Muraltia squarrosa</i>		2				<i>Anthospermum aethiopicum</i>	2	2	3	3	1
* <i>Clutia affinis</i>		2				<i>Gazania krebsiana</i> ssp. <i>krebsiana</i>					5
* <i>Brachiaria serrata</i>	4	5	1		1	<i>Thamnochortus fruticosus</i>					5
* <i>Indigofera denudata</i>	5	4				* <i>Helichrysum appendiculatum</i>	1		1	4	
* <i>Aspalathus chortophilla</i> ssp. <i>chortophilla</i>	4	4				<i>Pentastichis heptamera</i>					4
* <i>Hermannia flammea</i>	3	4	1			<i>Lobelia scabra</i>					4
<i>Selago glomerata</i>	4	2				<i>Commelina africana</i>	1			5	
* <i>Clutia brevifolia</i>	2	3				<i>Bulbostylis collina</i>	1			4	
* <i>Satyrium membranaceum</i>	2	3				<i>Helictotrichon hirtulum</i>	1			4	
* <i>Piloselloides hirsuta</i>	1	2				<i>Hypochoeris radicata</i>	1			4	
<i>Crassula ericoides</i> ssp. <i>ericoides</i>	2	3				<i>Helichrysum odoratissimum</i>	1	1		4	
<i>Helichrysum zeyheri</i>	2	3				<i>Scirpus antarcticus</i>					3
¹ <i>Erica demissa</i>	3	2				<i>Ficinia albicans</i>					3
<i>Alepidea capensis</i>			5			* <i>Arctopus echinata</i>					3
<i>Knowltonia capensis</i>		1	5			<i>Plagiocloa unioale</i>					3
<i>Clutia alaternoides</i>		1	5			<i>Cotula turbinata</i>					3
<i>Thamnochortus argenteus</i>			4			<i>Prismatocarpus strictus</i>					3
<i>Ehrharta ramosa</i>			4			<i>Setaria flabellata</i>	1			3	
<i>Helichrysum felinum</i>	1		4			<i>Aspalathus angustifolia</i>	1			3	
¹ <i>Psoralea polyphylla</i>		1	4			<i>Sporobolus africanus</i>					3
<i>Senecio oligoglossus</i>			3			<i>Oxalis polyphylla</i>	1			3	
* <i>Sporobolus centrifugus</i>			3			<i>Cynodon dactylon</i>	1			3	
<i>Berzelia intermedia</i>			3			<i>Muraltia ciliaris</i>				2	4
<i>Agathosma mundii</i>			3			* <i>Diheteropogon filifolius</i>				5	4
<i>Ursinia scariosa</i>			3			<i>Elegia vaginellata</i>				3	3
¹ <i>Senecio crenatus</i>	1	3				<i>Leonionyx glomerata</i>				3	2
¹ <i>Podalyria burchellii</i>	1	3				<i>Stoebe plumosa</i>			4		5
<i>Tetraria capillaceae</i>	1	3	1			* <i>Elionurus mutica</i>			3		3
<i>Rhus lucida</i>	1	3				* <i>Heteropogon contortus</i>		3			5
<i>Erica deliciosa</i>			2			* <i>Ehrharta calycina</i>		2			3
<i>Cannamois virgata</i>			2			* <i>Lasiocloa longifolia</i>	2	1			4
<i>Metelasia muricata</i>		4	3			<i>Restio triticeus</i>		5	5	5	5
<i>Protea neriifolia</i>		2	5			<i>Leucospermum cuneiforme</i>		1	3	4	2
<i>Watsonia meriana</i>		3	5			<i>Pentastichis curvifolia</i>		1	3	2	3
* <i>Helichrysum nudifolium</i>		2	3			* <i>Tristachya leucothrix</i>		2	1	1	5
<i>Pentastichis colorata</i>	5		3			* <i>Helichrysum anomalum</i>		3	1	1	1
<i>Merxmüllera stricta</i>	4		3			* <i>Cliffortia linearifolia</i>		1	1	1	2
¹ <i>Euryops munitus</i>	4		2	1	1	<i>Themeda triandra</i>	5	5	3	3	5
* <i>Ficinia tristachya</i>	4	4	3	1	1	¹ <i>Erica pectinifolia</i>	3	5	5	4	1
* <i>Trachypogon spicatus</i>	3	5	2	1	1	<i>Gnidia coriacea</i>	2	4	4	3	3
* <i>Bobartia orientalis</i>	2	4	5			* <i>Ficinia gracilis</i>	2	3	2	3	2
<i>Cymbopogon marginatus</i>	5	3	3	1	1	<i>Polygala microlopha</i>	2	1	1	2	1
<i>Elytropappus rhinocerotis</i>	5	3	3	1	1						
* <i>Rhus rosmarinifolia</i>	3	4	3		1						
* <i>Pentastichis angustifolia</i>	3	4	2		2						
<i>Erica diaphana</i>				5							
<i>Carpacoe vaginellata</i>				5							
<i>Thamnochortus glaber</i>				5							
<i>Tetraria circinalis</i>				4							
<i>Hypodiscus willdenowia</i>				4							
<i>Hypodiscus aristatus</i>				3							
<i>Penaea cneorum</i>				3							
<i>Cassytha ciliolata</i>	1		3								
<i>Tetraria compressa</i>	1	3	5								
<i>Lanaria lanata</i>	1	3	4		1						
¹ <i>Protea tenax</i>	1	2	3								

A : *Themeda triandra*-*Passerina pendula* Hankey Dry Grassy FynbosB : *Erica pectinifolia*-*Trachypogon spicatus* Humansdorp Grassy FynbosC : *Protea neriifolia*-*Clutia alaternoides* Humansdorp Grassy FynbosD : *Thamnochortus glaber*-*Erica diaphana* Tsitsikamma Grassy FynbosE : *Thamnochortus fruticosus*-*Tristachya leucothrix* Tsitsikamma Restioid Grassland

* Diagnostic species for Grassy Fynbos including:

¹ South Eastern endemics (Weimarck, 1941) largely restricted to Grassy Fynbos

and there is no evidence of thicket development in mature communities. Established thicket is extremely resistant to most fires: only thicket margin species are partially destroyed and they soon regenerate from epicormic buds (Martin, 1966). Furthermore, in the study area and elsewhere (see Martin, 1966), a predominantly grassy state in the post-fire succession of most Grassy Fynbos communities is very short-lived (6 - 12 months) after which post-fire resprouters start assuming dominance (Cowling, 1982b). Some of these fire-resistant resprouting species are regional endemics (e.g. Erica pectinifolia, Gnidia coriacea, Protea tenax, Phyllica gnidioides). Grassy Fynbos is not a derived vegetation type nor does it form a transitory successional stage between thicket and grassland. The implementation of a uniform fire régime combined with continuous, selective grazing has reduced the resilience (Holling, 1973; Walker et al., 1981) of these systems to a critical point where the "domains of attraction" (Holling, 1973) of populations are transcended resulting in shifts in patterns of dominance and local extinctions. I investigate these ideas more fully below and in Cowling (1982b).

3.1.2c Dynamics

In the study area nearly all Grassy Fynbos is presently burnt to a 4 to 5 year rotation. Vegetation is grazed soon after the fire by domestic livestock which select only young, growing grasses.

In prehistoric times grazing was probably irregular and localized and the fire régime more patchy (see 1.5). I have chosen the Erica-Trachypogon community (Figures 12 - 15) to illustrate the effect of different disturbance régimes on community composition and structure. Noble and Slatyer's (1980) vital attributes model was used to predict successional changes (Cowling, 1982b).

Species types in the Erica-Trachypogon community include those species which have the ability to rootsprout or sprout from a lignotuber and in which new recruitment only occurs immediately after a disturbance (VI species of Noble and Slatyer, 1980). Examples are Leucadendron salignum (cf. Williams, 1972), Leucospermum cuneiforme (cf. Rourke, 1972) and Erica pectinifolia (pers. obs.). CI species (e.g. Protea neriifolia, P. repens) are species having a storage of relatively long-lived propagules in the canopy of the individuals; new recruitment occurs only after a fire. The Protea spp. take 4 to 5 years to reach reproductive maturity and are not long-lived (20 - 30yr) (Rourke, 1980).



Fig. 13: Erica-Trachypogon Grassy Fynbos on shallow stony soil derived from Enon sandstones. Species include Protea neriifolia, Erica demissa, Themeda triandra, Trachypogon spicatus, Restio triticeus and Muraltia squarrosa. Near Hankey on road to Lorie (c. 150 m).



Fig. 14: Destruction by fire of a relic stand of Protea neriifolia in Erica-Trachypogon Grassy Fynbos. This stand included the only known population in the study area of the rare species Agathosma uncarpellata. Near Misgund (c. 200 m).



Fig. 15: Erica-Trachypogon Grassy Fynbos on red colluvial gravels (Hutton form). Frequently burnt and grazed. Species include Leucadendron salignum, Erica pectinifolia, Lanaria lanata, Themeda triandra, Restio triticeus, Leucospermum cuneiforme and Brachiaria serrata. Klipfontein mountains north of Humansdorp on road to Hankey (c. 300 m).

DI species are well dispersed (D), intolerant (I) species. Examples are Anthospermum aethiopicum and Cliffortia linearifolia. These species store seed in the soil and Cliffortia also resprouts from a rootstock (Martin, 1966). They start declining in importance after 8 to 10 years. The preponderance of I species stresses the importance of initial floristic composition (Connel and Slatyer, 1977) in determining patterns of secondary succession in Grassy Fynbos communities.

Fig. 16 shows the replacement sequence in the Erica-Trachypogon community under two disturbance régimes. Of great significance is that under a uniform fire régime, the model predicts that the CI species will be eliminated since second and later disturbances occur before juveniles mature, and propagules are poorly dispersed and short-lived (cf. Bond, 1980b). VI and DI species types are able to persist and become dominant under these conditions. These predictions are supported by field observations. On the Humansdorp coastal plain frequent burning has resulted in the elimination of fire-vulnerable seed regenerating species from the Erica-Trachypogon community (Figures 14 and 15). Near Hankey this community is not intensively grazed and fires are patchy and their frequency variable. CI species (Protea neriifolia, P. repens, Erica demissa (cf. Martin, 1966) dominate (Fig. 13). More details on the replacement sequence and implications of grazing are given in Cowling (1982b).

3.1.2d Grassiness

The grassiness of the eastern fynbos communities requires some discussion. Acocks (1953) and Kruger (1979) attribute it to a higher proportion of summer rain favouring the competitive growth of C4 tropical grasses. An alternative hypothesis is that the growth of predominantly deciduous C4 species is favoured on the more fertile eastern fynbos soils (cf. Heddle and Specht, 1975; Specht et al., 1977; Bond, 1981). The assumption implicit in this hypothesis, that C4 grasses are more competitive than, for example, Restionaceae under more fertile conditions, needs to be critically examined for local conditions.

A third hypothesis, related to the first mentioned, is that C4 grasses are favoured in those regions where temperatures are high during the growing season (Vogel et al., 1977). This hypothesis explains the high cover of C4 grasses on north slopes, even at high altitudes, since incoming radiation (and hence surface temperature) is highest on the north slopes during the equinoxes (Fig. 7) which coincide with rainfall peaks (Fig. 4).

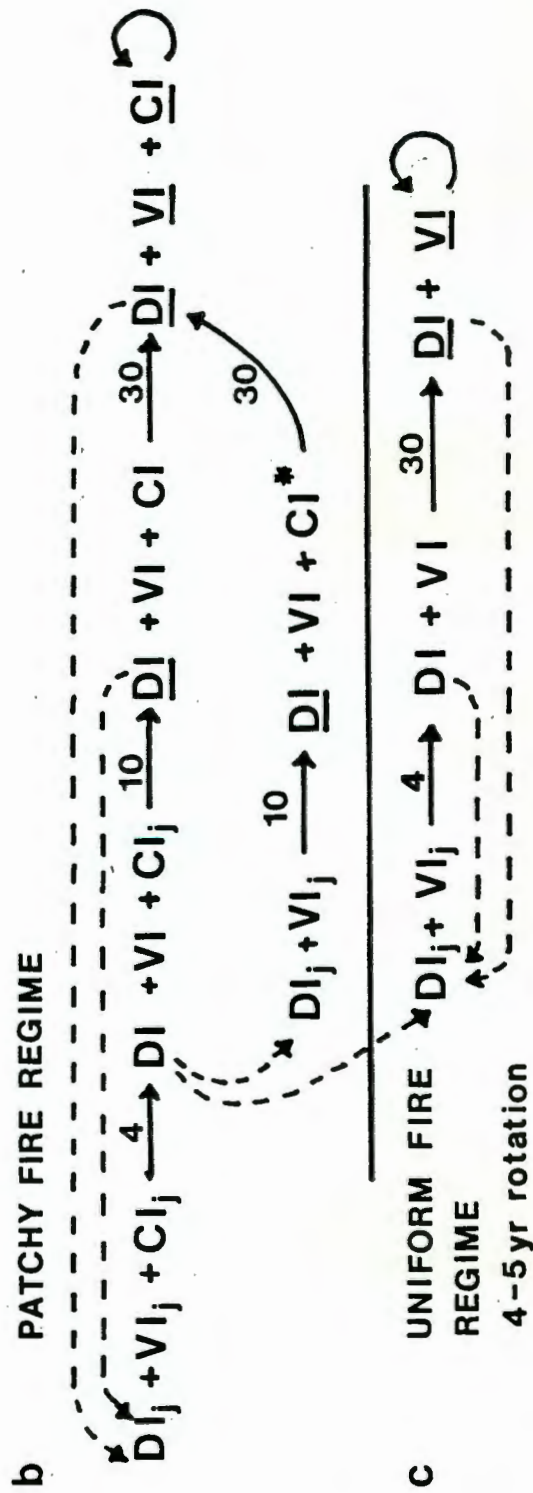
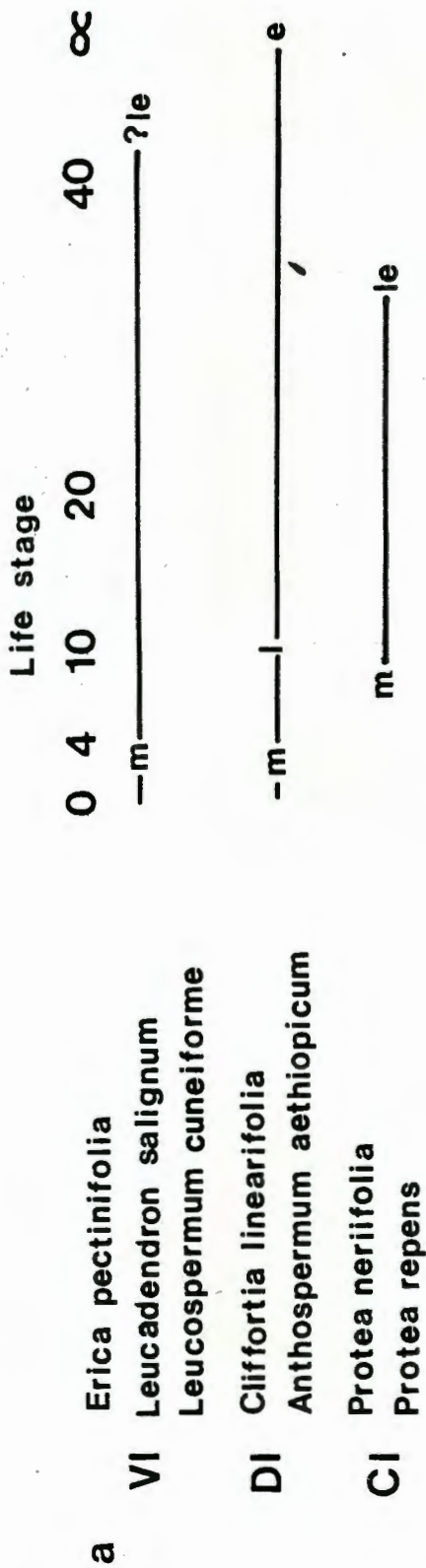


Fig. 16.

Vegetation replacement sequence for the *Erica-Trachypogon* Grassy Fynbos communities. Figure 16a summarises the vital attribute data required to derive the replacement sequences under a patchy fire régime (Fig. 16b) and a uniform fire régime (Fig. 16c) (see text). Life stage parameter characteristics are: m, time to reach reproductive maturity; l, the longevity of the population; and e, the longevity of the propagule pool. Underlined species types indicate that component species are moribund but not locally extinct. *represents the limited dispersal of CI propagules from adjacent unburned vegetation (only possibly under a patchy fire régime). Subscript j indicates species in juvenile (premature) stage.

On southern slopes at high altitudes temperatures during the growing season are lower and Restionaceae predominate (Cowling and Campbell, 1982b). The hypothesis also explains the decline in grass cover with increasing age of Grassy Fynbos communities (Cowling, 1982b). Shade cast by the overstorey creates a cooler microclimate at ground level favouring species with low optimum temperatures for growth (C3 grasses and Restionaceae); burning destroys this effect resulting in higher soil temperatures which favour C4 grasses (cf. Rice and Parenti, 1978). The assumption that dominant Restionaceae (e.g. Restio triticeus) outcompete C4 grasses at lower growing season temperatures should be tested experimentally. Bond (1980a) and Pierce and Cowling (in prep.) have found that in the southern and south eastern Cape respectively R. triticeus grows in the cooler, winter months.

Patterns in the relative coverage of C3 and C4 grasses are also explained by the growing season temperature hypothesis (Cowling, 1982g). In Grassy Fynbos C3 grasses comprise on average about one third of the total grass cover (Cowling, 1982g). This relative coverage increases with vegetation age and on cool southerly slopes, indicating a microclimatic lowering of growing season temperatures, favouring the competitive growth of C3 species. In the study area C3 grasses persist as a usually minor component of mature Grassy Fynbos, long after most C4 species have declined and virtually disappeared (Cowling, 1982g).

3.1.2e Synonymy

Phytocoenoses conforming to my concept of Grassy Fynbos have been described from Albany Zuurberg and quartzitic forelands by Dyer (1937 - Fynbos), Martin and Noel (1960 - Erica demissa mixed heath alliance), Martin (1965 - mature Erica demissa heath, Erica demissa-Phyllis axillaris heath, Tetraria capillacea mixed dwarf shrub heath) and Jessop and Jacot Guillarmod (1969 - Macchia - grassveld). Olivier (1977) gives a brief description of Grassy Fynbos near Port Elizabeth and some of Phillips' (1931) lithophilous macchia in the Knysna district is Grassy Fynbos. At this stage it is uncertain whether the Grassy Fynbos concept could include the Protea nitida communities ('Waboomveld') described by Bond (1981) in the Outeniquas and Taylor and Van der Muelen (1981) in the Rooiberg. Campbell's (1982b) Grassy Fynbos concept is essentially a structural one; he includes C3 grass dominated types from the south western Cape and excludes grassy communities with proteoid overstoreys.

3.1.2f Communities in the study area

I have described five Grassy Fynbos communities from the study area (Table 5). The Themeda-Passerina community (Fig. 17) is transitional between Grassy Fynbos and Coast Renosterveld. It is a species-rich and highly variable community occurring on stony Oakleaf soils derived from Enon conglomerate, and is restricted to the southern wall of the Gamtoos valley where the rainfall is between 400 and 500 mm yr⁻¹. The Erica-Trachypogon community occurs on the T.M.G. sandstones of the coastal plain (Figures 12, 14, 15) and on Enon sandstones in the Gamtoos region between Hankey and Loerie (Fig. 13). Soils are litholic, infertile sandy loams (Glenrosa, Hutton (stony phase) forms). Rainfall is 500 - 600 mm yr⁻¹. The community occurs in two structural cover states : one dominated by resprouting fire-resistant species (Fig. 15), the other dominated by seed-regenerating species (Fig. 13) (see below). The Protea-Clutia community occupies the southern slopes of the low quartzite hills northwest of Humansdorp which receive a higher rainfall (600 - 700 mm yr⁻¹) than the surrounding plains. Soils are shallow Mispah and Glenrosa forms on upper slopes and stony Hutton form on lower slopes. Structural cover states similar to the Erica-Trachypogon community were identified. The Thamnochortus-Erica (Fig. 18) community occurs on deep well-drained and highly leached sands (Constantia form) south of the Kromme river. This community is entirely dominated by resprouting species. Rainfall is 650 - 750 mm yr⁻¹. The Thamnochortus-Tristachya community is a restioid grassland on deep seasonally water-logged sands of pediments and valley fills in the Oyster Bay-Cape St. Francis region (Fig. 19) and immediately north and west of Humansdorp (Fig. 20). Fig. 21 shows a schematic soil and vegetation catena including the two last-mentioned communities. Details on the floristic and environmental interrelationships of Grassy Fynbos communities in the study area are given in Cowling (1982b).

3.1.3 South Coast Dune Fynbos

The current concept of Coastal Fynbos (47) includes a heterogeneous group of vegetation types. Acocks (1979) subdivided Coastal Fynbos into west and south coast blocks but acknowledges that further subdivision is needed. Taylor (1978) and Kruger (1979²) have largely adopted Acocks' scheme in their treatment of the Coastal Fynbos.



Fig. 17: Themeda-Passerina Dry Grassy Fynbos on shallow loamy sands on Enon conglomerate. Species include Protea repens, Elytropappus rhinocerotis, Leucadendron salignum, Passerina pendula, Themeda triandra, Restio cuspidatus and Phylica abutina. Brandkoppes above the Gamtoos River (c. 150 m).



Fig. 18: Thamnochortus-Erica Grassy Fynbos three years after a fire. Gentle north slope above Kromme river (c. 60 m). Soil is a deep, well-drained sand (Constantia form) and is very infertile. Dominant shrubs all resprouting from lignotubers. (Erica diaphana, E. pectinifolia, Leucadendron salignum, Leucospermum cuneiforme). Graminoids include Tetraria compressa, Hypodiscus willdenowia, Restio riticeus and Diheteropogon filifolius. Linderhof, between Cape St. Francis and Oyster Bay.



Fig. 19: Thamnochortus-Tristachya Restioid Grassland on deep, seasonally waterlogged sands (Longlands form). Dominant species include Thamnochortus fruticosus, Heteropogon contortus, Tristachya leucothrix and Elionurus mutica. Buffelsbos, between Cape St. Francis and Oyster Bay (c. 80 m).



Fig. 20: Restioid Grassland on pediment below the Klipfontein mountains, north west of Humansdorp. Soil is a deep, seasonally waterlogged sand overlying a ferricrete hardpan. Dominant species are Themeda triandra, Thamnochortus fruticosus, Elegia sp., Helictotrichon hirtulum, Heteropogon contortus and Helichrysum anomalum. Rondebosch (c. 220 m.)

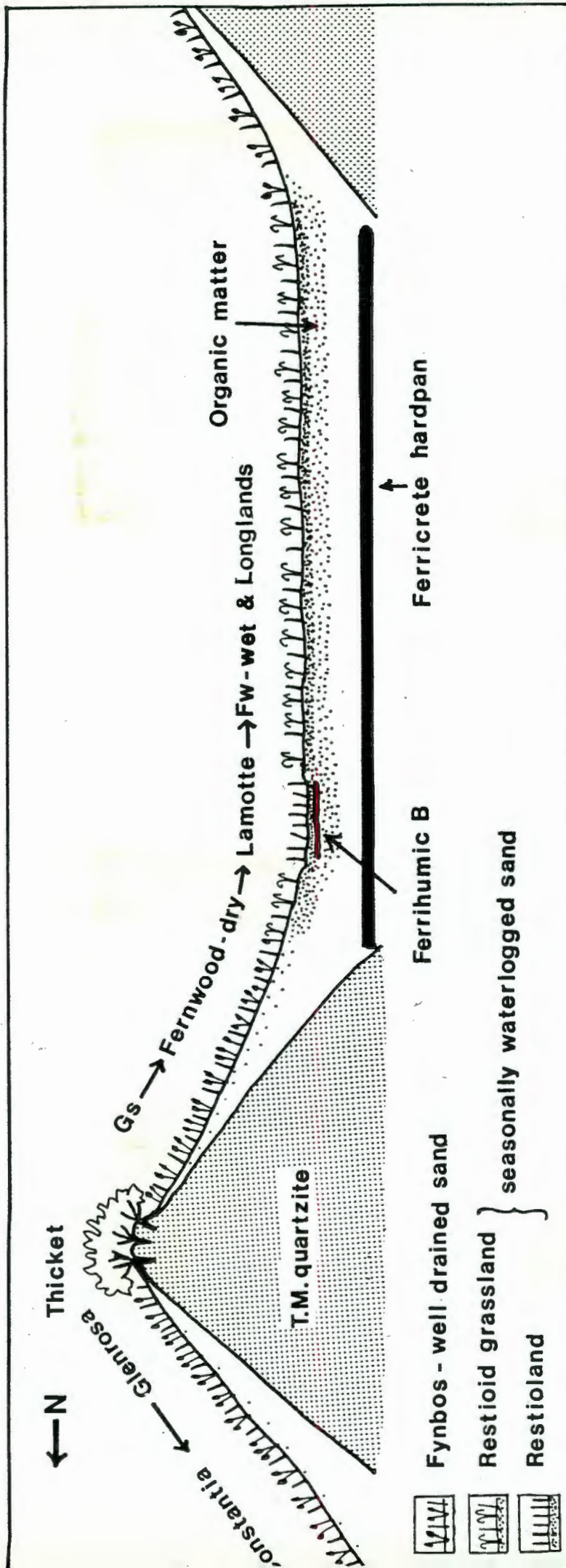


Fig. 21. Schematic soil and vegetation catena on the coastal foreland (T.M.G.) south of the Kromme river. Communities are fynbos (Thamnochortus-Erica community) and restioid grassland (Thamnochortus-Tristachya community).

There are at least four fundamental types of Coastal Fynbos. Acocks (1953) has long recognised that the dwarf fynbos of the Elim flats should be considered a distinct veld type. The south coast calccrete fynbos centred between Bredasdorp and Mossel Bay is another well circumscribed type (Acocks, 1953; Taylor, 1978). These communities are restricted to calcareous, neutral to alkaline, shallow sands overlying calccrete of the Bredasdorp Formation, and are characterized by a great number of endemics (see Taylor, 1978, for a partial list). Van der Merwe (1977) has described communities from the De Hoop Nature Reserve and Muir (1929) gives a general account of calccrete fynbos in the Riversdale district. Another group of Coastal Fynbos communities occurs on deep, acid, infertile sands and is mainly confined to the west coast (cf. Milewski and Esterhuyzen, 1977; Boucher, 1982) but also occur locally on the south coast (e.g. sandy flats vegetation on reddish sands in the Riversdale district; Muir, 1929). These Coastal Fynbos types are structurally similar to Mountain Fynbos. The presence of tall tufted Restionaceae (Thamnochortus spp., Willdenowia striata) and a greater importance of geophytes and annuals in the calccrete and acid sand fynbos and the occurrence of subtropical thicket species (Rhus, Euclea) in the former, could be regarded as diagnostic features.

A fourth type, which I define below, is South Coast Dune Fynbos. Communities belonging to this order occur on Recent, deepish, calcareous sands from the Cape Flats to Cape Recife, near Port Elizabeth. They are characterized by good diagnostic species including Euclea racemosa ssp. racemosa, Restio eleocharis, R. leptoclados and Agathosma apiculata (Table 6). South Coast Dune Fynbos is further characterized by a strong component of non-fynbos shrubs and trees which links it to the Tongaland-Pondoland dune thicket (e.g. Rhus crenata, Olea exasperata, Maytenus procumbens, Rhoicissus tridentata, Sideroxylon inerme) (Fig. 9; Table 6; see also Moll and White, 1978). Proteaceae are usually lacking.

Structurally South Coast Dune Fynbos is distinguished from other fynbos orders by the strong component of large-leaved dorsiventral shrubs (subtropical species mentioned above) and the lack of proteoid shrubs (Fig. 10). Although grass cover can be quite high, restioids and small-leaved shrubs dominate in the herb and shrub strata respectively. According to Campbell's (1982b) structural criteria, communities in the study area would be classified as fynbos.

TABLE 6. South Coast Dune Fynbos Communities

Community Number of relevés	A 5	B 13	C 12	Community Number of relevés	A 5	B 13	C 12
* <i>Stenotaphrum secundatum</i>	5	1	1	* <i>Agathosma apiculata</i>		1	3
<i>Themeda triandra</i>	5	2		<i>Ficinia ramosissima</i>			3
<i>Cynodon dactylon</i>	5	2	1	<i>Cassytha ciliolata</i>		1	2
<i>Sporobolus africanus</i>	4	2		* <i>Salvia aurea</i>		1	2
<i>Geranium incanum</i>	4	1		* <i>Restio leptoclados</i>		3	4
<i>Vigna unguicallata</i>	4			<i>Cymbopogon marginatus</i> ¹	1	3	3
<i>Hermannia althaeoides</i>	4	1		<i>Sutera campanulata</i>		3	3
<i>Cullumia decurrens</i>	3		1	* <i>Sutera microphylla</i>		3	2
<i>Setaria flabellata</i>	3	2		* <i>Myrica quercifolia</i>		2	3
<i>Ficinia indica</i>	3			* <i>Rhus crenata</i>		2	4
<i>Centella coriacea</i>	3	1		* <i>Ficinia aphylla</i>		3	2
<i>Cotula sericea</i>	3	1		<i>Metalasia muricata</i>		2	3
<i>Silene primulifolia</i>	3			* <i>Restio eleocharis</i>	3	5	4
¹ <i>Agathosma stenopetala</i>		4	1	<i>Anthospermum aethiopicum</i>	4	4	3
<i>Muraltia squarrosa</i>		4	2	<i>Helichrysum teretifolium</i>	2	4	5
<i>Tetraria cuspidata</i>	2	4	2	* <i>Euclea racemosa</i> ssp. <i>racemosa</i>	2	4	5
* <i>Limonium scabrum</i>		4	1	<i>Passerina vulgaris</i>	3	4	4
<i>Disparago ericoides</i>		3	1	* <i>Rhus glauca</i>	3	3	5
<i>Pelargonium urbanum</i>		3	2	¹ <i>Felicia echinata</i>	2	4	4
<i>Psoralea bracteata</i>	2	2	1	<i>Chironia baccifera</i>	3	2	4
<i>Erica glumiflora</i>		2		* <i>Rhus laevigata</i>	3	3	3
<i>Ficinia albicans</i>		2		* <i>Imperata cylindrica</i>	2	3	2
<i>Linum thunbergii</i>		2		¹ <i>Rapanea gilliana</i>	2	3	3
¹ <i>Erica chloroloma</i>		2		<i>Carpobrotus deliciosus</i>	2	2	3
* <i>Myrica cordifolia</i>	1	2		¹ <i>Phyllica litoralis</i>	4	1	3
* <i>Stipagrostis zeyheri</i> ssp. <i>zeyheri</i>		2		<i>Tephrosia rapensis</i>	4	2	1
* <i>Chondropetalum microcarpum</i>	1	2	2	<i>Helichrysum cymosum</i> ssp. <i>cymosum</i>	3	2	1
<i>Linum africanum</i>	4	2	1	<i>Melica racemosa</i>	3	2	1
* <i>Lasiachloa obtusifolia</i>	4	2		¹ <i>Pentaschistis heptamera</i>	3	3	1
<i>Oxalis polyphylla</i>	4	2					
¹ <i>Satyrium princeps</i>	4	2	1				
<i>Senecio burchellii</i>	4	2	1				
<i>Gazania krebsiana</i> ssp. <i>krebsiana</i>	3	3					
<i>Thesium strictum</i>	2	2					
<i>Aspalathus spinosa</i> ssp. <i>spinosa</i>	2	2	1				
<i>Indigofera stricta</i>	2	2	1				
<i>Hebenstreitia integrifolia</i>	2	2	1				
¹ <i>Polygala ericaefolia</i>	1	2	1				
* <i>Maytenus procumbens</i>			5				
* <i>Olea exasperata</i>		2	5				
* <i>Cassine tetragona</i>	1	1	4				
* <i>Rhoicissus tridentata</i>			4				

A : *Themeda triandra*-*Stenotaphrum secundatum*
South Coast Dune Grassland

B : *Restio eleocharis*-*Agathosma stenopetala*
Tsitsikamma Dune Fynbos

C : *Restio eleocharis*-*Maytenus procumbens*
Tsitsikamma Dune Fynbos/Thicket

* Diagnostic species for South Coast Dune Fynbos, including:
¹ South Eastern endemics (Weimarck 1941) largely restricted to Dune Fynbos (Tsitsikamma group)

Taylor (1978) and Boucher and Moll (1980) partially include my concept of South Coast Dune Fynbos with strandveld, a large-leaved thicket of subtropical affinity. They do this because of the complex successional interplay between fynbos and thicket communities. On deep well-drained sands secondary succession proceeds from a fynbos to a thicket cover state with a mixed fynbos/thicket mid-successional state (Cowling, 1982a). On shallower sands overlying calcrete, fynbos communities, identical to the early fynbos state on deep sands, persist without any invasion of thicket elements. While recognising these successional relationships, I have chosen to place the thicket and fynbos states in separate orders.

South Coast Dune Fynbos communities have been described from the Cape Flats by Taylor (1972 - Metalasia coast dune fynbos), from Cape Hangklip by Boucher (1978 - Ehrharta-Ficina Strand Pioneer community), from Groenvlei by Martin (1960 - dune heath) from Goukamma by Van der Merwe (1976 - Helichrysum teretifolium - Metalasia muricata shrubland community, Tetraria cuspidata - Restio eleocharis fynbos community), from Robberg by Taylor (1970a - Phyllica-Passerina microphyllous Evergreen Steppe Coast Fynbos, Metalasia-Restio Gray Evergreen Microphyllous Shrub Pseudo-Savanna) and from near Port Elizabeth by Olivier (1979 - Coastal fynbos intermingled with scrub).

Phillips (1931) gives a general account of South Coast Dune Fynbos (Psammophillous macchia) from the Knysna region and Muir (1929) describes some communities from the Riversdale district. Possible outliers occur on the west coast near Langebaan (Metalasia-Myrica Dune Dense Evergreen Ericoid Shrubland; Boucher and Jarman, 1977) and east of Port Elizabeth (Dyer, 1937 - Psammophillous macchia; Martin and Noel, 1960 - Maritime heath).

I recognised three South Coast Dune Fynbos Communities in the study area (Table 6). The Themeda-Stenotaphrum community occurs on deep seasonally-waterlogged sands in dune valleys (Fig. 22) and also on well-drained sands subjected to frequent bush-cutting (Fig. 23). In the latter areas, in the absence of bush-cutting, the community develops from a closed grassland to small-leaved shrubland and thicket; in the dune valleys the establishment of shrubland is prevented by abnormally high watertable years when fynbos initials such as Passerina vulgaris, Metalasia muricata, Anthospermum aethiopicum and Aspalathus spinosa ssp. spinosa are killed (pers. obs.). Despite the tropical affinity of the grass flora and some of the forbs, the presence of many Dune Fynbos diagnostic species (Table 6) and strong successional relationships links the Themeda-Stenotaphrum to the South Coast Dune Fynbos.



Fig. 22: Themeda-Stenotaphrum Dune Grassland (foreground) on deep seasonally waterlogged sands (Fernwood form). Dune thicket on well-drained deep sands (dune ridge) in background. Grassland species include Themeda triandra, Restio eleocharis, Imperata cylindrica, Aspalathus spinosa, Rapanea gilliana and Tetraria cuspidata. Cape St. Francis (c. 20 m).



Fig. 23: Dune Grassland, Fynbos and Thicket complex on deep well-drained sands. Grassland maintained by frequent bush-cutting. Grassland species include Stenotaphrum secundatum, Themeda triandra, Tristachya leucothrix, Rhoicissus tridentata and Thamnochortus glaber. Brandewynkop near Oyster Bay (c. 100 m).



Fig. 24: Restio-Agathosma Dune Fynbos on well-drained deep, yellow-brown sands (Clovelly form). Dominant ericoid shrub is Passerina vulgaris. Other species include Muraltia squarrosa, Metalasia muricata, Agathosma stenopetala, Restio eleocharis, Stipagrostis zeyheri and Ehrharta calycina. Brandewynkop near Oyster Bay (c. 80 m).

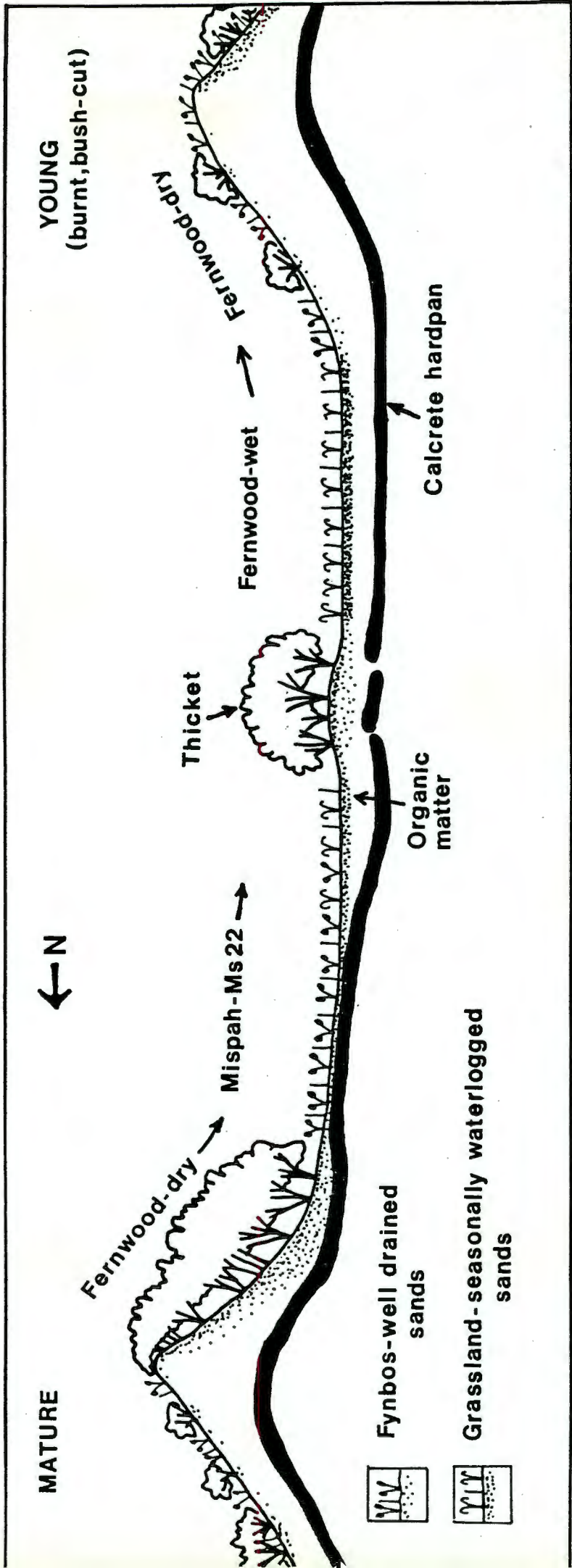


Fig. 25. Schematic soil and vegetation catena on linear dune topography near Cape St. Francis.

The Restio-Agathosma community (Figs. 24, 37) is found on well-drained deep sands (Fernwood form) on dune ridges, where it is successional to thicket, and on shallower well-drained sands overlying calcrete (Mispah form). The lack of thicket development in the latter area is probably due to the inability of thicket species to outcompete shallow-rooted fynbos species where rooting depth is limited to 50 cm or less, and that the shallow soils are droughty. The Restio-Maytenus community is a Small-leaved Shrubland/Large-leaved Shrubland (thicket) confined to deep well-drained sands on dune ridges where it often replaces the Restio-Agathosma community in a successional sequence to dune thicket. Fig. 25 shows a schematic soil and vegetation catena on linear dunes near Cape St. Francis. Details on the floristic and environmental interrelationships and the dynamics of South Coast Dune Fynbos communities are given in Cowling (1982a).

3.2 Cape Transitional Small-leaved Shrublands

Within and adjacent to the Fynbos Biome are a variety of non-succulent Small-leaved Shrublands which, according to the concepts developed above, are distinctly non-fynbos. Although some of these shrublands have been the subject of a recent review (Boucher and Moll, 1980) there are no published phytosociological surveys and the formulation of syntaxonomic concepts is therefore severely limited. I tentatively define Cape Transitional Small-leaved Shrublands as follows:

- (i) Phytochorological spectra are dominated by ecological and chorological transgressor species linking the Cape region with adjacent phytochoria, particularly the Karoo-Namib and Afromontane regions. Cape endemics comprise about one third of a given sample flora (Fig. 9).
- (ii) Regional endemism is lower than for Cape Fynbos Shrublands and many endemics are not members of typical Cape genera (Fig. 9).
- (iii) Structurally the communities are Small-leaved Shrublands but they lack most of the "heathland" (sensu Specht, 1979) features typical of Cape Fynbos Shrublands. Restioid and proteoid growth forms are almost entirely lacking and grasses dominate in the field layer (Fig. 10). Deciduous geophytes are prominent, if not in cover, then in richness. A considerable proportion of the small-leaved woody shrubs have fleshy (semi-succulent) leaves (Fig. 10) and some show seasonal leaf dimorphism. Shrubs with large dorsiventral leaves are occasional.

- (iv) Ecologically they are restricted to fine grained soils derived from Cretaceous mudstones and conglomerates, Malmesbury and Congo phyllites, Bokkeveld shales, Cape Granites and the tillites and shales of the Karoo System (Table 3). The soils are generally more fertile than Cape fynbos soils (Fig. 8). Cape Transitional Small-leaved Shrublands are found in areas receiving at least 30% winter rain where the annual average precipitation is from 300 - 600 mm (Table 3).

Characteristic genera of Transitional Small-leaved Shrublands are Relhania, Elytropappus, Aspalathus, Euryops, Pteronia, Passerina, Eriocephalus, Selago, Hermannia and Helichrysum.

I include the following Acocks' (1953) veld types: Coastal Renosterbosveld (46), Mountain Renosterbosveld (43) and parts of the Karroid Merxmuellera Mountain Veld (60). The last mentioned has strong links with Afromontane grasslands of the north eastern Cape (Acocks, 1953). Campbell's (1982b) Renosterveld, Clanwilliam Karroid Shrubland and much of his Grassy Shrubland are Cape Transitional Small-leaved Shrublands.

I present here the outline of an hypothesis to explain the origin of Cape Transitional Small-leaved Shrublands (for details see Cowling, 1982e). Implicit in this thesis is the assumption that the junction between the shale derived soils of the coastal forelands and the sandy, infertile soils of the T.M.G. quartzites forms an effective migration barrier under most climatic conditions. I assume that under moister conditions than present, there was limited movement of fynbos taxa onto the shale derived coastal foreland soils and that under drier conditions fynbos on the mountains was not greatly displaced by karroid shrublands. The general tenet of this assumption is that this soil fertility barrier served to isolate the mountains as a series of "islands" with respect to the adjacent lowland flora. Extreme climatic differences between the mountains and lowlands reinforces this effect.

Transitional Small-leaved Shrublands occupy tension zones between adjacent phytochoria: between the Cape and Karoo-Namib regions but also between these and the Afromontane and Tongaland-Pondoland regions (Fig. 26). They are often dominated by one or two generalist species (DI species type of Noble and Slatyer, 1980) such as Elytropappus rhinocerotis (renosterbos), Metalasia muricata, Relhania spp. and Euryops spp. These species are widely distributed, are able to grow under a wide range of conditions and have "weedy" characteristics (Levy, 1926; 1935a; Trollope, 1970; 1980). They are mostly derived from Cape taxa. Elytropappus is a Cape genus of six species: five have fairly

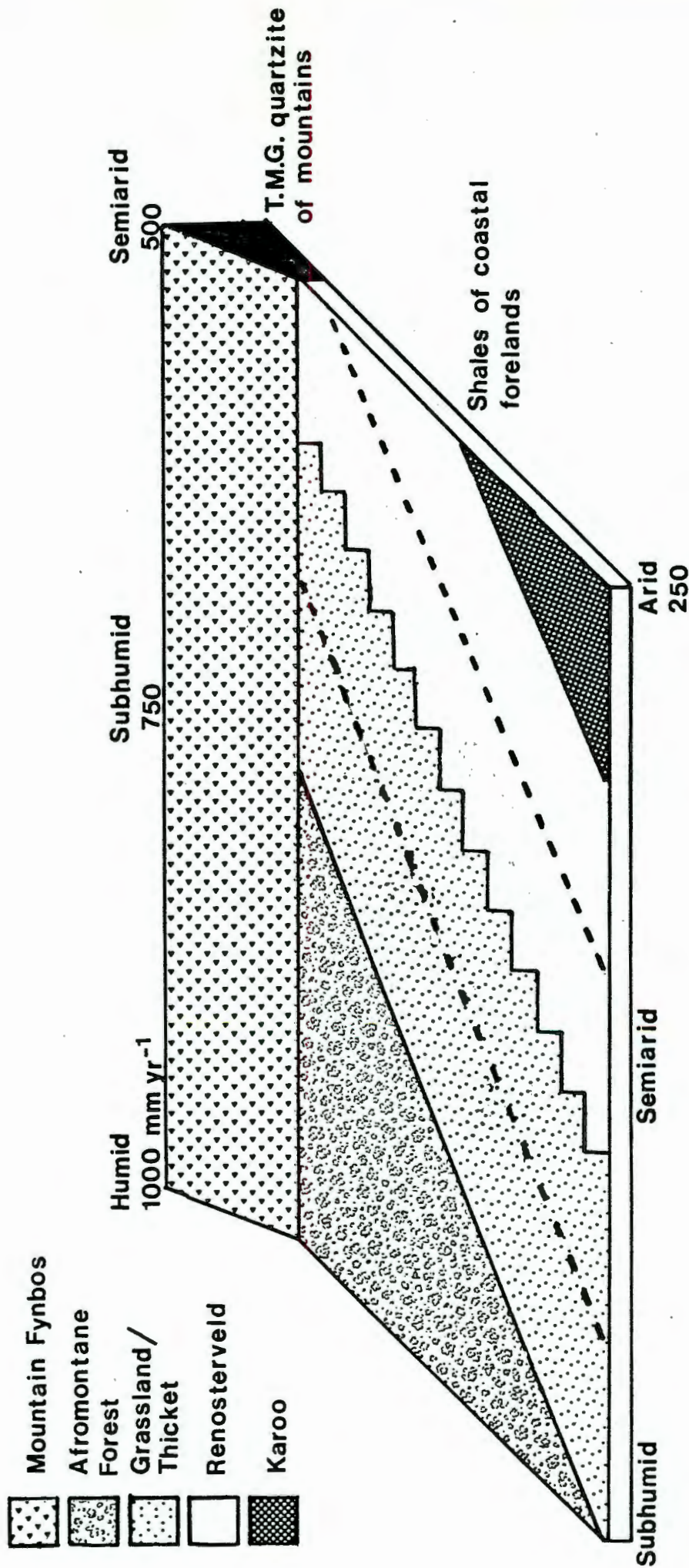


Fig. 26. Renosterveld on the south coast forelands as a tension zone vegetation. Renosterveld communities occupy a zone between karoo and grassland/thicket. The location of this zone would change with climatic fluctuations, and disappear under arid conditions when karoo reached the T.M.G./shale junction. Dashed lines define a sensitive zone vulnerable to mismanagement and the establishment of "false" shrublands.

localized distributions in the south western Cape while E. rhinocerotis is widely distributed throughout the Cape Region, the Great Escarpment of the south central Cape and parts of the eastern Cape (Levy, 1927). Similarly Metalasia is a Cape genus of 33 species, most of which have restricted distributions in the Cape Region (Pillans, 1954). M. muricata is a wide-ranging "weedy" species common in certain Transitional Small-leaved Shrublands (Cowling, 1982c).

The tension zone occupied by Transitional Small-leaved Shrublands would have been unstable during Late Cainozoic climatic fluctuations. During the last glacial, when conditions were drier than at present (Deacon, 1982), the expansion of karroid shrublands on the coastal forelands would have eliminated these transitional shrublands in places; in other regions they would have expanded at the expense of grassland and thicket/forest (Cowling, 1982e).

The instability of this tension zone is likely to have favoured the establishment of weedy species which were recruited from adjacent phytochoria (cf. Gibbs Russell and Robinson, 1981).

In drier regions marginal to karroid shrublands, Transitional Small-leaved Shrublands are regarded as "natural" communities (Acocks, 1953). I suggest that under these conditions E. rhinocerotis and other shrubs would occupy most niches, as species with more mesic requirements were eliminated prior to the invasion of karoo. In moister, bimodal rainfall regions, where Transitional Small-leaved Shrublands are marginal to grasslands of tropical affinity, man-induced disturbances have telescoped these events by creating environments which are effectively more arid and by minimizing competition through the selective utilization of species by domestic livestock (Fig. 26). I describe below the recent spread of E. rhinocerotis in South Coast Renosterveld.

The hypothesis I have presented above has many testable predictions. Palynological studies such as those being undertaken by Deacon and associates in the southern Cape (e.g. Deacon, 1979) will undoubtedly be of value in determining the historical sequence of vegetation types. Demographic studies to determine the population strategies of the major shrub species and other autecological investigations may explain the competitive "superiority" of these species. Of interest, too, is the possible role of allelopathy: Squires and Trollope (1979) have clearly demonstrated the allelopathic effects Chrysocoma tenuifolia, the principal invasive species of false karroid shrublands and a component of drier Transitional Small-leaved Shrublands.

However, most important at this stage are detailed phytosociological studies to clarify the biogeographical and ecological relationships of these shrubland communities.

3.2.1 South Coast Renosterveld

Acocks (1953; 1979) recognizes two coastal renosterveld types: a west coast form and a south coast form. This distinction has been upheld by Taylor (1978) and Boucher and Moll (1980).

West coast renosterveld differs from the south coast form in having a sparser grass cover composed largely of C3 genera (Ehrharta, Pentaschistis, Merxmuellera, Lasiochloa), a higher diversity of deciduous geophytes and annuals and the presence of Relhania ericoides and Leyssera gnaphaloides as characteristic subdominants with Elytropappus rhinocerotis. West coast communities have a stronger fynbos influence, especially on granitic soils. Boucher (1982) has suggested that west coast renosterveld is derived from Mountain Fynbos.

South Coast Renosterveld ranges from the Caledon district to Humansdorp with outliers on the Albany coastal forelands (Table 3). Unlike the west coast form, South Coast Renosterveld receives a considerable amount of summer rain. Typical subdominants and diagnostic shrub species are Relhania genistaefolia, R. cuneata, Helichrysum anomalum, Indigofera denudata and Hermannia flammea (Table 7). Tropical C4 grasses, which do not reach the west coast, are particularly common (Fig. 9, Table 7).

Acocks' (1953) conjecture that the original vegetation of the South Coast Renosterveld was a scrub forest (thicket) (see Acocks, 1953; p.8, Map 1, p. 86) is not corroborated by historical accounts and the habitat requirements of present-day thicket "relics".

Judging from the earliest records it appears that much of the South Coast Renosterveld was a dense Themeda triandra dominated grassveld. The south coast forelands were once known as the "blougrasveld", a reference to the blueish hue of the once common Themeda (Smit, 1943). However, as early as 1775, Sparrman (1785) noted the demise of the grasslands and the spread of Elytropappus rhinocerotis. He attributed this to the continuous overgrazing of the grassveld by domestic livestock (see also Hall, 1934; Levyns, 1935b; Du Toit and Du Toit, 1938; Smit, 1943; Levyns, 1956).

TABLE 7. South Coast Renosterveld communities

Community Number of relevés	A 11	B 12	C 10	D 4	Community Number of relevés	A 11	B 12	C 10	D 4
<i>Arctopus echinatus</i>	4	1			<i>Polygala microlopha</i>		2	1	
* <i>Cliffortia linearifolia</i>	4	2			<i>Piloselloides hirsuta</i>	3	4	3	
<i>Restio sieberi</i>	4	1			* <i>Passerina rubra</i>	3	2	4	
* <i>Gladiolus longicollis</i>	4				* <i>Oxalis smithiana</i>	2	2	2	
<i>Drosera aliciae</i>	4				<i>Asparagus capensis</i>	3	1	2	
<i>Oxalis polyphylla</i>	3	1			* <i>Relhania genistaefolia</i>			1	5
<i>Spiloxene minuta</i>	3				<i>Merxmüllera disticha</i>		1		5
<i>Cotula turbinata</i>	3				<i>Felicia filifolius</i>				5
* <i>Selago canescens</i>	3				<i>Euclea undulata</i>				3
<i>Tetraria cuspidata</i>	2				<i>Putterlickia pyracantha</i>				3
* <i>Gnaphalium repens</i>	2				<i>Asparagus striatus</i>			2	4
¹ <i>Erica unilateralis</i>	2				* <i>Argyrolobium collinum</i>		3	3	
* <i>Gazania linearis</i> ssp. <i>linearis</i>		4			<i>Aspalathus lactea</i> ssp. <i>adelphea</i>			3	3
<i>Clusia rubicaulis</i>	1	3	1		* <i>Argyrolobium pumilum</i>			2	3
<i>Ornithogalum minus</i>	1	2			<i>Eriocephalus africanus</i>			1	3
<i>Senecio oederiaefolius</i>	1	2			* <i>Indigofera denudata</i>		3	4	5
<i>Euryops munitus</i>		2			* <i>Cymbopogon marginatus</i>		3	5	4
* <i>Helichrysum odoratissimum</i>	5	3	2		<i>Oxalis punctata</i>		4	3	4
* <i>Babiana patersoniae</i>	5	3			* <i>Hermannia flammea</i>		5	3	2
* <i>Helichrysum nudifolium</i>	3	5			* <i>Thunbergia capensis</i>		2	3	3
<i>Pelargonium dichondraefolium</i>	3	4			<i>Indigofera heterophylla</i>	3	5		5
* <i>Crassula ciliata</i>	4	2			<i>Tephrosia capensis</i>	3	4		4
<i>Euclea crispa</i>	2	4			* <i>Helictotrichon hirtulum</i>	4	4		3
<i>Oxalis purpurea</i>	3	2			* <i>Helichrysum teretifolium</i>	2	2		5
<i>Schoenoxiphium caricoides</i>	2	3			<i>Aspalathus spinosa</i> ssp. <i>spinosa</i>	2	3		3
* <i>Pelargonium hirsutum</i>	2	2			* <i>Metalasia muricata</i>	1	4		2
<i>Corymbium africanum</i>	1	3			* <i>Anthospermum aethiopicum</i>	1	3		2
* <i>Eustachys paspaloides</i>			5		* <i>Disparago ericoides</i>	1	3		2
<i>Helichrysum zeyheri</i>			5		* <i>Themeda triandra</i>	5	5	5	4
<i>Commelina africana</i>			5		<i>Hibiscus pusillus</i>	4	4	5	4
¹ <i>Lampranthus productus</i>			4		<i>Elytropappus rhinocerotis</i>	4	4	5	5
¹ <i>Bobartia orientalis</i>	2	1	4		* <i>Pentstemon angustifolia</i>	5	4	5	3
¹ <i>Hypoxis stellipilis</i>			4		<i>Anthospermum ciliare</i>	4	4	5	3
¹ <i>Metalasia aurea</i>		1	4	2	* <i>Ficinia tristachya</i>	3	4	5	4
<i>Ficinia nigrescens</i>			4		* <i>Chaetacanthus setiger</i>	4	3	3	4
* <i>Trachypogon spicatus</i>			3		* <i>Satyrium membranaceum</i>	4	5	2	4
¹ <i>Blepharis procumbens</i>			3		* <i>Sporobolus africanus</i>	5	3	2	4
* <i>Crassula ericoides</i> ssp. <i>ericoides</i>			3		<i>Cynodon dactylon</i>	5	2	2	4
<i>Lightfootia rubens</i>			3		* <i>Helichrysum aromatum</i>	2	4	5	2
<i>Babiana sambucina</i>			3		* <i>Brachiaria serrata</i>	2	2	5	2
¹ <i>Drosanthemum gracilimum</i>			3		* <i>Eragrostis capensis</i>	2	2	3	2
<i>Digitaria eriantha</i>			3		<i>Lasiachloa longifolia</i>	2	1	4	4
<i>Carum capense</i>			3		<i>Selago corymbosa</i>	2	2	1	4
¹ <i>Hermannia sulcata</i>			3		<i>Ledebouria cooperi</i>	2	2	2	3
¹ <i>Walafrida nitida</i>			2						
<i>Thesium flexuosum</i>			2						
<i>Haplocarpa lyrata</i>			2						
¹ <i>Monechma acutum</i>			2						
<i>Asparagus densiflorus</i>			2						
* <i>Barleria pungens</i>		3	5						
* <i>Clusia brevifolia</i>		3	5						
<i>Sutera pinnatifida</i>		3	4						
<i>Senecio othonniflorus</i>		2	2						
<i>Rhynchosia totta</i>		2	2						

A : *Themeda triandra*-*Cliffortia linearifolia*

Humansdorp False Fynbos

B : *Elytropappus rhinocerotis*-*Metalasia muricata*

Humansdorp Coast Renosterveld

C : *Elytropappus rhinocerotis*-*Eustachys paspaloides*

Hankey Coast Renosterveld

D : *Elytropappus rhinocerotis*-*Relhania genistaefolia*

Humansdorp Coast Renosterveld

* Diagnostic species for South Coast Renosterveld including:
¹ South Eastern (Weimarck, 1941) and Kaffrarian Transition
Zone (Cowling, 1982e) endemics largely restricted to South
Coast Renosterveld and related grasslands

A study of the present-day distribution of thicket in the Coast Renosterveld of the study area (Cowling, 1982c) shows that it is always restricted to deep, well-drained soils; renosterveld and grassveld are generally confined to shallow soils, often with poorly-developed clayey, impermeable subsoils (Glenrosa and Swartland forms) (Figures 27 - 29). Only a few shallow rooted thicket species (Rhus glauca, R. lucida, R. incisa and Euclea crispa) are occasionally associated with renosterveld.

I suggest that South Coast Renosterveld is derived from grassveld and that thicket was always subordinate in the landscape where it was restricted to special edaphic sites largely centred along river courses and on rock outcrops and termitaria of the interfluvies. The advent of settled agriculture shifted the disturbance régime from pulse disturbance grazing and variable fire intervals to a fixed burning cycle and continuous overgrazing (1.5). Continuous immediate post-fire grazing which was widely practised, is particularly harmful to the grass sward (Du Toit and Du Toit, 1938; Smit, 1943; Smith, 1967). The increased predictability of the disturbance régime led to a reduced resilience of the system (cf. Walker et al., 1981). As resilience is lowered, there is usually a critical point where slight increases in mortality can trigger population collapses, i.e. populations are forced close to the boundary of their "domain of attraction" and then "flip" over it (Holling, 1973). In this way the system shifted from a grass dominated state to a shrub dominated one.

In the study area there are some fenceline contrasts separating grassland and shrubland cover states of the same community (Figures 30 - 32). Pure grasslands are maintained by occasional heavy grazing in a rotational system employing a large number of small camps. This encourages a mat-like growth of Themeda with a high basal density and the development of a Cynodon dactylon sward which effectively binds the soil and minimizes bare soil patches. Renosterveld communities on the Bokkeveld shale flats south of Humansdorp occur on duplex soils which are seasonally waterlogged. Continuous overgrazing of the grass sward causes soil capping which results in increased run-off, the truncation of topsoils and the eventual disturbance of water table dynamics (Fig. 29). This process favours the establishment of woody species (Tinley, 1977). Once established, the elimination of E. rhinocerotis and other species is difficult as they have deep roots (Scott and Van Breda, 1937) which are able to utilize relatively reliable subsoil moisture. This moisture is not normally available to shallow rooted grasses in the droughty topsoils. Shrubs must be removed by fire or mechanical means but are often re-established within a few years (Levyns, 1935b; Cowling, 1982c).



Fig. 27: Elytropappus-Metalasia Renosterveld on eroded duplex soils (Glenrosa and Swartland forms). Thicket along drainage line and on termitaria in background. Renosterveld species include Elytropappus rhinocerotis, Themeda triandra, Hermannia flammea and Metalasia muricata. Thicket species are Olea europaea, Tarchonanthus camphoratus, Rhus lucida and Pittosporum viridiflorum. Above Seekoie river, south of Humansdorp (c. 80 m).



Fig. 28: Elytropappus-Eustachys Renosterveld (grassland cover state) on shallow loamy sands on Enon conglomerate. Species include Themeda triandra, Trachypogon spicatus, Metalasia aurea, Helichrysum anomalum, Eustachys paspaloides and Elytropappus rhinocerotis. Thicket in background on termitaria. Papiesfontein (c. 70 m).

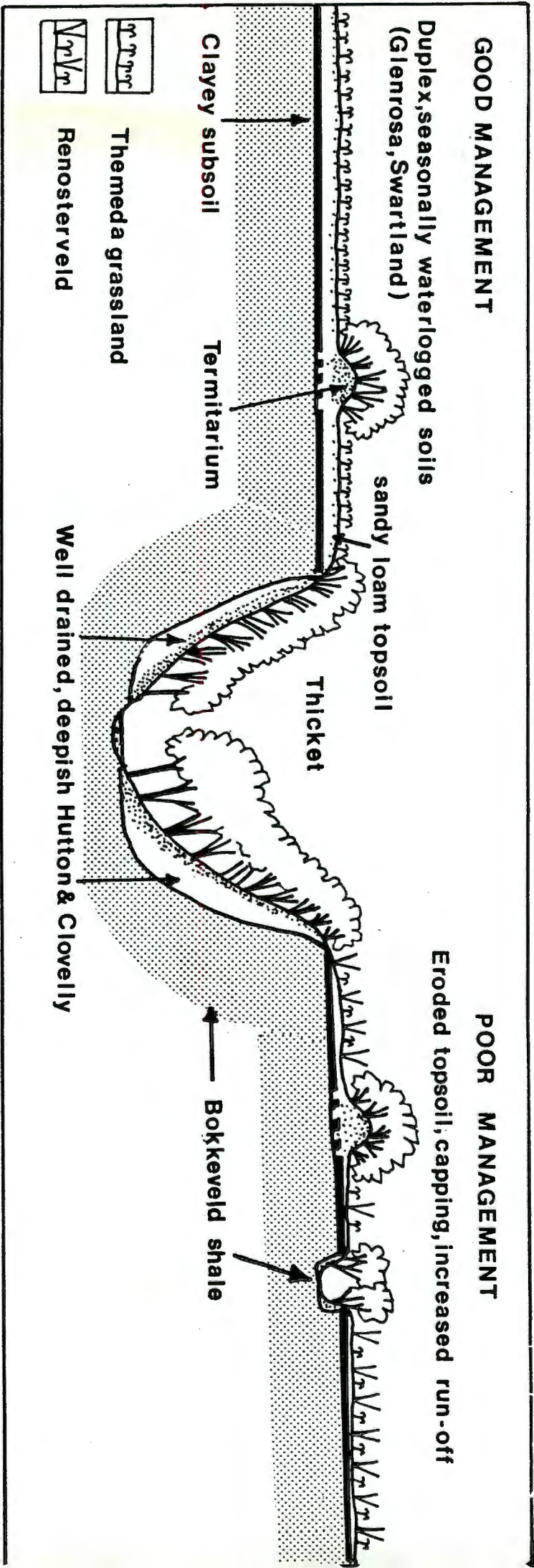


Fig. 29. Schematic soil and vegetation catena on the Bokkeveld shale flats, south of Humansdorp.



Fig. 30: Overgrazed Cliffortia-Themeda False Fynbos on shallow sandy loam overlying a poorly developed clayey subsoil (Glenrosa form) on Bokkeveld shale. Beyond fenceline in background is high watertable Themeda grassland. Dominant species in foreground: Cliffortia linearifolia, Themeda triandra, Sporobolus africanus, Gnaphalium repens, Rhus incisa and Restio sieberi. Osbosch near Kromme river mouth (c. 30 m).



Fig 31: Grassland and shrubland cover states on the Themeda-Cliffortia False Fynbos community. Grassland is pure and exceptionally dense. Species include Themeda triandra (dominant), Helictotrichon hirtulum, Pentascistis angustifolia, Sporobolus africanus, Festuca caprina, Setaria flabellata and Restio sieberi. Grassmere, between Humansdorp and Cape St. Francis (c. 50 m).

Communities belonging to the South Coast Renosterveld have been described from the Swellendam district by Grobler and Marais (1967 - Renosterbos community of the plains, Renosterbos - Themeda community), from near Riversdale by Taylor (1970b - Elytropappus Evergreen Microphyll Shrub Steppe Savanna). General accounts of the South Coast Renosterveld are given by Muir (1929) for the Riversdale district and Jordaan (1947) for the Caledon and Bredasdorp districts. The Acacia karroo-Themeda triandra association of Martin and Noel (1960) and the Acacia karroo savanna of Jessop and Jacot-Guillarmod (1969) have many diagnostic renosterveld species. These communities occur on Bokkeveld shales on the Albany forelands. Mismanagement often results in the co-dominance of E. rhinocerotis and Acacia karroo (pers. obs). I have sampled a renosterveld community on Dwyka shales, north of Grahamstown (unpublished data). Dominant species included Elytropappus rhinocerotis, Felicia filifolia, Aspalathus lactea ssp. adelphea, Relhania genistaefolia and Themeda triandra (cf. Table 7).

I have described four South Coast Renosterveld communities from the study area (Table 7). These communities are difficult to characterize since variation in type and intensity of recurrent disturbances is reflected in variations in species composition (Cowling, 1982c).

The Themeda-Cliffortia community is confined to the wetter ($550 - 650 \text{ mm yr}^{-1}$) parts of the Bokkeveld shale flats, along the Kromme river. The community consists of two structural cover states: a Closed Grassland dominated by Themeda and a derived Small-leaved (Grassy) Shrubland dominated by Cliffortia linearifolia (Figures 30 and 31). Soils are shallow, duplex types (Glenrosa and Swartland forms) which are waterlogged in winter. Destruction of the grass sward and subsequent topsoil erosion has adversely affected the water-table dynamics (see above).

The strong Afromontane affinities of this community (e.g. Helichrysum odoratissimum, Cliffortia linearifolia, Festuca spp., Gladiolus longicollis) link it to Afromontane fynbos and grassland (see Story's (1952) Cliffortia linearifolia lowland macchia and Killick's (1963) Cave Sandstone Scrub). Species of Cape affinity include Leucadendron salignum, Erica unilateralis, Tetraria cuspidata and Restio sieberi. This community best fits the concept of false or derived fynbos as formulated by Acocks (1953). Structurally these communities would not be classified as fynbos by Campbell (1982b). Due to the presence of diagnostic renosterveld species in the Themeda-Cliffortia community (Table 7) I have included it in South Coast Renosterveld.



Fig. 32: Fenceline contrast showing shrubland and grassland cover states of the Elytropappus-Metalasia Renosterveld community. Duplex soils on Bokkeveld shale (Glenrosa to Swartland forms). Note thicket development (Rhus glauca) along fenceline which affords a perch for frugivorous birds. Near Aloe Ridge at Aston Bay (c. 20 m).



Fig. 33: Degraded Themeda-dominated grassland being invaded by Elytropappus rhinocerotis (Elytropappus-Metalasia community). Bokkeveld shale flats between the Kromme and Seekoie rivers (c. 30 m).



Fig. 34: Elytropappus-Eustachys Renosterveld (shrubland cover state) on Enon conglomerate. Dominant species include Elytropappus rhinocerotis, Passerina rubra, Aspalathus chortophilla, Themeda triandra, Eustachys paspaloides and Pentaschistis angustifolia. Papiesfontein (c. 40 m).

I have observed allied communities with C. linearifolia as a dominant on the Coastal Platform between George and Groot Brak, in the Zuurberg and the Amatole mountains (cf. Story, 1952). In the eastern Cape these communities do not indicate a massive eastwards movement of fynbos elements in historical times (cf. Acocks, 1953; Trollope, 1970; 1973) but rather a localized thickening up of species present in the pre-disturbance grasslands, albeit in restricted habitats.

The Elytropappus-Metalsia community (Figures 27, 32 and 33) occurs in the drier regions ($450 - 550 \text{ mm yr}^{-1}$) of the Bokkeveld shale flats on shallow duplex soils. Grassland and shrubland cover states have been identified (Cowling, 1982c). The Elytropappus-Relhania community is restricted to the driest regions ($400 - 450 \text{ mm yr}^{-1}$) of the Coastal Platform above the Gamtoos River valley. Soils are mostly deep (0,8 - 1,0 m) Hutton form.

The Elytropappus-Eustachys community (Figures 28 and 34) is exceptionally species rich and chorologically complex. It is restricted to Enon conglomerates on the coastal forelands. Soils are stony well-drained loamy sands and are slightly less fertile than renosterveld soils derived from Bokkeveld shale (Fig. 8). Many relevés from this community are transitional to the Themeda-Passerina Grassy Fynbos community (3.1.2).

Details of the floristics, structure and environmental interrelationships of the renosterveld communities are given in Cowling (1982c).

3.3 Subtropical Transitional Thicket

Closed Large-leaved Shrublands (sensu Campbell et al., 1981) of essentially tropical and subtropical affinity penetrate into the Fynbos Biome from the east and extend along the west coast as far as Lamberts Bay. Physiognomically these shrublands consist of an impenetrable tangle of shrubs and low trees usually interwoven by woody climbers. Communities of similar structure and generic composition are found throughout tropical and subtropical Africa (Okali et al., 1973; Tinley, 1975; White, 1982) and are termed thicket. Tinley (in Heydorn and Tinley, 1980) extended the thicket concept to the Fynbos Biome. Boucher and Moll (1980) call Fynbos Biome thicket communities mediterranean shrublands, a clearly erroneous interpretation, since affinities are strongly tropical and there are virtually no thicket species endemic to the Cape mediterranean-climate region (Cowling, 1982e).

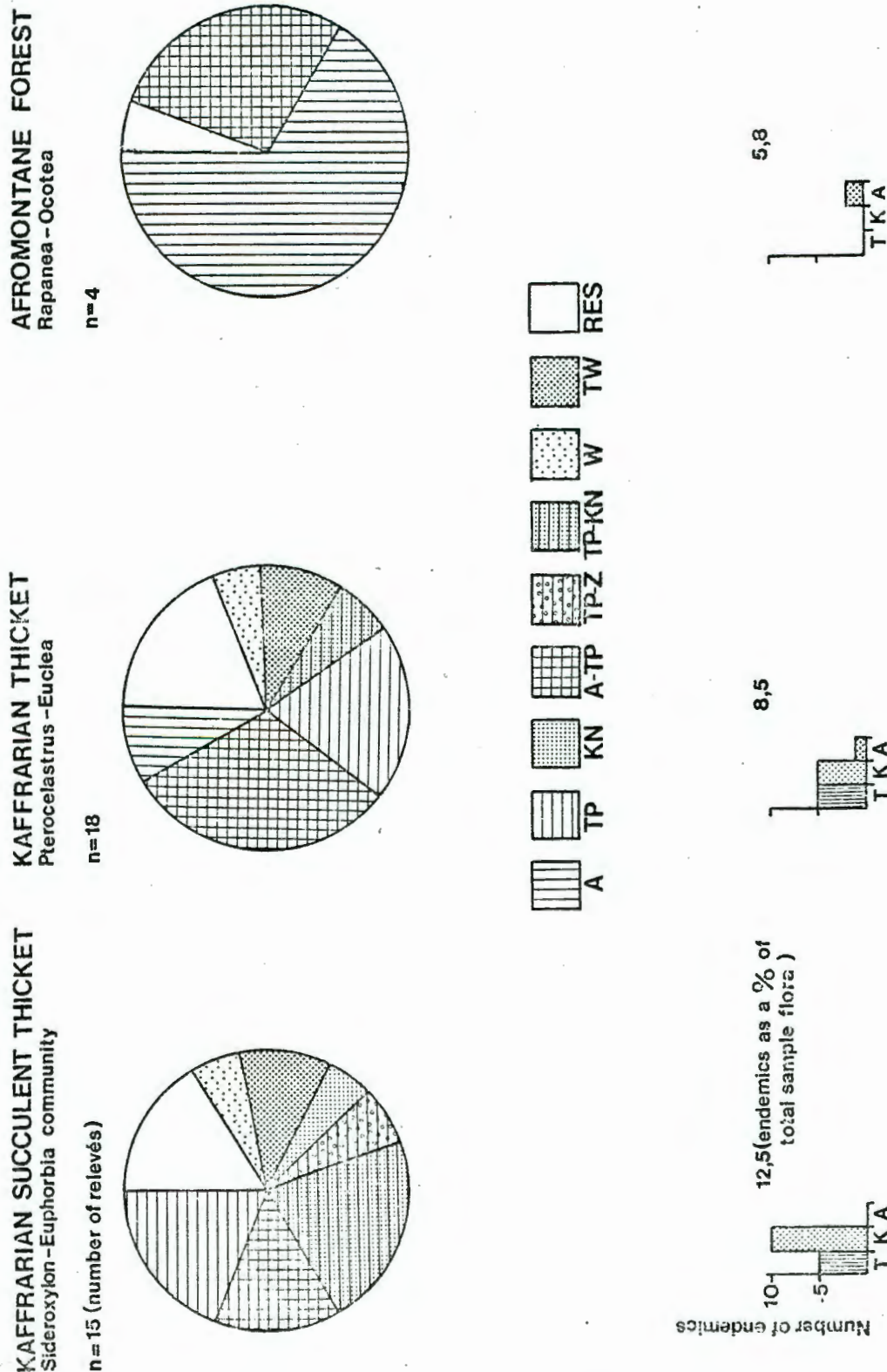
Subtropical Transitional Thicket occurs roughly from the Kei River to the south western Cape (Table 3). I define it as follows:

- (i) Phytochorological spectra are dominated by ecological and chorological transgressor species linking the Tongaland-Pondoland Region with Afromontane, Karoo-Namib and to a lesser extent, Cape regions. Tongaland-Pondoland endemics comprise about one-quarter of a given sample flora (Fig. 35).
- (ii) Regional endemics are few and usually of non-tropical affinity. Karroid shrubs, particularly succulents (Euphorbia, Crassula, Delosperma, Aloe) comprise most of the endemics (Fig. 35).
- (iii) Structurally the communities are dominated by large-leaved evergreen sclerophyllous shrubs many of which are stem-spinescent. Succulents are conspicuous in dry areas and vines are generally common (Fig. 36).
- (iv) Ecologically Subtropical Transitional Thicket is restricted to deepish, well-drained fertile soils (Fig. 8, Table 3). Transitional Thicket occurs in areas which receive at least some winter rain.

Subtropical Transitional Thicket includes thicket in Acocks' (1953) Southern Form of the Eastern Province Thornveld (7b), False Thornveld Eastern Cape (21), Southern Variation of the Valley Bushveld (23b), Fish River Scrub (23c), Addo Bush (23d(i)), Sundays River Scrub (23d(ii)), Gouritz River Scrub (23e), Noorsveld (24), as well as thicket in Dense Strandveld Scrub (34a), Coastal Rhenosterbosveld (46) and Coastal Macchia (47).

Also included are certain scree and rock outcrop communities in Mountain Fynbos (69 and 70).

Transitional Thicket has few character taxa. A list of trees and tall shrubs includes Euclea racemosa ssp. racemosa, E. polyandra, E. tomentosa, Maytenus lucida, M. oleoides, Cassine maritima, C. reticulata, Rhus longispina, R. crenata, R. schlechteri, Cussonia gamtoensis, C. thyrsoflora, Olea exasperata, Rapanea gilliana, Heeria argentea, Maurocena frangularia, Brachylaena neriifolia, Aloe africana and Euphorbia tetragona. Many of these are derived from species more widely distributed in the tropics and subtropics (e.g. Robson, 1966 for Maytenus and F. White pers. comm. for Euclea). The drier succulent form of the Transitional Thicket has a number of endemic succulent shrubs of karroid affinity, belonging to the genera Delosperma, Senecio, Euphorbia, Crassula, Zygophyllum and Lampranthus.



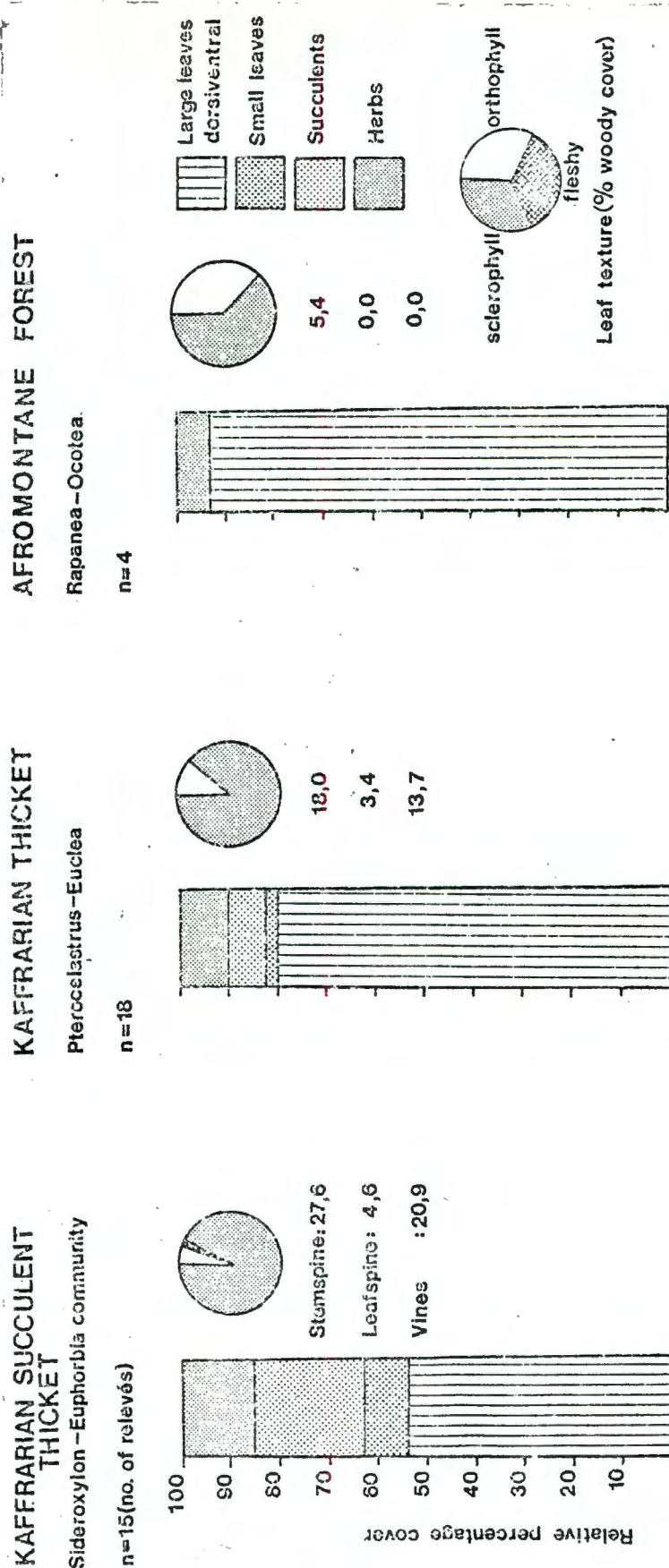


Fig. 36: Growth form composition of Subtropical Transitional Shrublands and Afromontane Forest.

The general trend within the Transitional Thicket flora is a drastic depauperization westwards. Of the tropical and sub-tropical shrub and tree species reaching the Kei River, 49,5% do not extend beyond the Kaffrarian Transition Zone (2.2.4) (Cowling, 1982e; see also Gibbs Russel and Robinson, 1981). In the study area, which is on the western boundary of the transition zone, there are 97 non-succulent thicket shrubs and trees; on the south and west coast forelands there are 43 and 24 species respectively (data from Muir, 1929; Acocks, 1953; 1979; Boucher and Jarman, 1977; pers. data).

Structurally, Transitional Thicket is readily distinguished from other African thicket types. There is a predominance of evergreen sclerophyllous leaves (Fig. 36) and a high cover of succulent shrubs of karroid affinity. Thicket communities to the north often have a strong component of orthophyllous deciduous species (Wild, 1952; Edwards, 1967; Fanshawe, 1968; Tinley, 1977). Winter deciduousness is a predictable strategy of tropical summer-rainfall climates (cf. Orians and Solbrig, 1977). However in the south eastern Cape where rainfall distribution is highly erratic (Gibbs Russel and Robinson, 1981) and in the southern and south western Cape where a high proportion of the rain falls in winter, plants must be capable of utilizing soil moisture whenever its availability coincides with other optimum growth conditions. Clearly long-lived, sclerophyllous "high-cost - slow-profit" leaves (Orians and Solbrig, 1977) will be favoured (Cowling and Campbell, 1982a).

The distribution of thicket communities is determined by a complex of interrelated factors. Fire is cited as a factor limiting the distribution of thicket in the eastern south eastern Cape (Du Toit, 1972; Trollope, 1974). Thicket is often restricted to what are usually interpreted as fire protected sites (scree, rock outcrops, ravines, termitaria and river valleys). Trollope (1974) emphasizes the historic role of fire and browsing ungulates in restricting thicket development.

Tinley (1977; in Heydorn and Tinley, 1980) stressed edaphic controls on the distribution of thicket. Thicket development is often restricted to deep well-drained soils. In a study of thicket clump formation on the Accra Plains, Ghana, Okali *et al.* (1973) conclude that thicket is restricted to deep, uniform, finely-grained soils; surrounding grassland occurs on a shallow duplex soil (sandy topsoil) which is seasonally waterlogged. In my study area the densest thicket occurs on deep apedal sandy loams to sandy clay loams (Hutton and Clovelly forms) derived from Enon shales and mudstones. The soils are well drained and probably capable of retaining much moisture at the rooting depth of the thicket species. Thicket is also found on dune sands, termitaria, stable talus and

scree slopes, rock outcrops and river valleys. All these sites are characterized by deep, well drained soils. These profiles probably offer the rooting depth and water retaining capacity necessary for thicket formation (cf. Okali *et al.*, 1973; Tinley, 1977).

It has been shown that the soils of thicket clumps, especially when they are associated with termitaria, are more fertile than the soils of surrounding vegetation (Watson, 1967; Fanshawe, 1968; Okali *et al.*, 1973; Fig. 8). The association of thicket and termite mounds is a constant feature throughout sub-Saharan Africa (e.g. Wild, 1952; Fanshawe, 1968). It has been suggested that termitaria favour thicket formation by providing fire protection for woody plants and by improving soil nutrient, drainage and water storage conditions (Lee and Wood, 1971; Trapnell *et al.*, 1976; Tinley, 1977). On non-termitarium sites it is possible that the higher fertility status of the soils is due to plant-induced soil changes resulting from increased litter accumulation and decomposition (cf. Paulsen, 1953; Charley and West, 1976; Aweto, 1981). Correlative studies of soil variables show strongly significant positive relationships between organic carbon and major nutrients in thicket soils suggesting plant-induced enrichment (Cowling, 1982 a-d). There are strong indications that a build up in organic matter is a prerequisite for thicket formation (Cowling, 1982c).

Most thicket species have fleshy fruits which are mainly bird dispersed (Bews, 1917; Tinley, 1977; pers. data). Avian dispersal undoubtedly plays an important role in the establishment of thicket particularly in the vicinity of perches (rock outcrops, termitaria, established thicket) (Bews, 1917; Tinley, 1977). Many of these perch sites also fulfil the edaphic requirement for thicket initiation.

Fire, edaphic factors and dispersal agents all contribute to the dynamics of thicket formation. Fire protection is of critical importance in the early stages of thicket initiation but becomes less important as the thicket matures. The roles of soil depth, drainage and organic matter, and dispersal agents have not been adequately stressed as factors contributing to the development of Transitional Thicket. A more fruitful approach to the study of the structure and dynamics of Fynbos Biome thicket communities is to look to the work on subtropical and tropical African thicket and not to studies of mediterranean shrublands on other continents.

Post disturbance dynamics of Transitional Thicket communities in the study area were not studied. Thicket communities are stable and have low resilience. They regenerate slowly after occasional catastrophic disturbances such as fire or clearing, and are

eliminated if these disturbances occur at intervals of less than a few decades.

The thicket communities are not fire prone but are vulnerable to overstocking of domestic livestock, particularly goats (Aucamp and Barnard, 1980).

3.3.1 Kaffrarian Thicket

Kaffrarian Thicket consists of the non-succulent Subtropical Transitional Thicket communities. They have their maximum expression in the Kaffrarian Transition Zone and depauperate outliers extend to the south western Cape.

Kaffrarian Thicket has strong affinities with the Afromontane Forest flora although Tongaland-Pondoland endemics and linking species dominate the phytochorological spectrum; endemism is low (Fig. 35). Structurally the thicket is a closed shrubland to low forest dominated by evergreen, sclerophyllous trees and shrubs with a high cover of stemspines and vines (Fig. 36). Some diagnostic species are listed in Table 8.

Included in Kaffrarian Thicket are the thickets in Acocks' (1953) Eastern Province Thornveld (7b), Alexandria Forest (2), False Thornveld of Eastern Cape (21), Coastal Rhenosterbosveld (46) and Coastal Macchia (47). Without the relevant data I cannot say how far westwards the Kaffrarian Thicket extends. It is possible that the scree thickets in Mountain Fynbos, with character species such as Maytenus oleoides, Heeria argentea, Euclea polyandra and Maurocena frangularia should be placed in a separate order within the Subtropical Transitional Thicket.

Kaffrarian Thicket occurs on a wide range of parent materials, wherever conditions are suitable. At a later stage, it may be possible to subdivide it into alliances representing dune thicket, clay thicket and mountain thicket. Kaffrarian Thicket on dunes ranges from the Algoa Bay coast to the Cape Peninsula and is characterized by a number of species largely restricted to deep, calcareous, coastal dune sands (e.g. Olea exasperata, Euclea racemosa ssp. racemosa, Rhus crenata, Maytenus procumbens, Cassine maritima). It must be distinguished from the more tropical Mimusops caffra-Brachylaena discolor dune thicket of the Natal and Transkei coasts (Acocks, 1953; Moll and White, 1978). Dune thicket communities are described from the Algoa Bay coast by Taylor and Morris (1981 - Olea exasperata Bush, Pterocelastrus tricuspidatus Bushclumps, Dune woodland), from Goukamma by Van der Merwe (1976 - Sideroxylon inerme community), from Robberg by Taylor (1970 a - Mesophyllous Evergreen Broad Sclerophyll Mixed Coastal Scrub), from De Hoop Nature Reserve by Van der Merwe (1977 - Sideroxylon inerme forest and

TABLE 8. Kaffrarian Thicket communities

Community Number of relevés	A 12	B 5	C 11	D 18	Community Number of relevés	A 12	B 5	C 11	D 18
* <i>Cynanchum obtusifolium</i>	5				<i>Schoenoxiphium sparteum</i>			3	4
<i>Cussonia thyrsiflora</i>	4				* <i>Lachnostylis hirta</i>			3	3
<i>Secamone alpinii</i>	3				* <i>Senecio deltoideus</i>			3	3
² <i>Olea exasperata</i>	3				* <i>Olea europaea</i>			2	4
* <i>Clausena anisata</i>	3	1			* <i>Allophylus decipiens</i>			3	2
* <i>Dovyalis rotundifolia</i>	3	1			* <i>Maytenus acuminatus</i>			3	2
<i>Azima tetracantha</i>		4			<i>Hypoestes verticillaris</i>			3	2
<i>Asparagus suaveolens</i>		4			<i>Plectranthus madagascariensis</i>			2	3
<i>Schotia afra</i>	1	4			* <i>Cassine peragua</i>	3		5	2
<i>Aloe africana</i>	2	4			<i>Rhus longispina</i>	1	5	2	5
<i>Zygophyllum morgsana</i>		3			<i>Cotyledon velutina</i>	1	5	2	3
<i>Euphorbia mauritanica</i>		3			<i>Cassine aethiopica</i>	5	5	5	4
<i>Capparis sepiaria</i>		3			<i>Scutia myrtina</i>	4	5	5	5
<i>Canthium spinosum</i>	1	3			* <i>Pterocelastrus tricuspidatus</i>	5	3	5	5
² <i>Euclea racemosa</i> ssp. <i>racemosa</i>	3	3			<i>Carissa bispinosa</i>	5	2	5	5
* <i>Zanthoxylon capense</i>	3	3			<i>Rhaicissus digitata</i>	3	5	5	4
* <i>Aloe arborescens</i>			5		<i>Panicum obumbratum</i>	3	4	5	5
* <i>Gonioma kamassi</i>			4		<i>Sideroxylon inerme</i>	5	4	2	4
* <i>Canthium inerme</i>			4		<i>Rhoiacarpos capensis</i>	3	3	4	5
* <i>Maytenus nemorosa</i>			4	1	<i>Cassine tetragona</i>	3	3	3	5
* <i>Podocarpus falcatus</i>			3		<i>Grewia occidentalis</i>	2	3	3	4
<i>Oxalis stenorrhynca</i>			3		<i>Putterlickia pyracantha</i>	5	2	2	3
<i>Asparagus macowanii</i>			3		<i>Rhus glouca</i>	3	2	3	2
* <i>Vepris undulata</i>			3						
¹ <i>Smelloyphyllum capense</i>			3						
* <i>Dovyalis rhamnoides</i>			3						
* <i>Plectranthus verticillaris</i>			3						
* <i>Apodytes dimidiata</i>			3	1					
* <i>Burchellia bubalina</i>			2						
<i>Linociera foveolata</i>	3		5						
<i>Euclea undulata</i>			1	5					
<i>Maytenus heterophylla</i>				3					
<i>Schotia latifolia</i>				3					
<i>Ochna serrulata</i>				2					
<i>Panicum deustum</i>	2	4		3					
<i>Sclopia zeyheri</i>	3	1		4					
<i>Euphorbia triangularis</i>	3	1		3					
* <i>Euclea racemosa</i> ssp. <i>macrophylla</i>			5	5					
* <i>Dietes iridiodes</i>			5	4					
<i>Asparagus setaceus</i>			5	4					
<i>Hippobromus pauciflorus</i>			3	5					
<i>Asparagus aethiopicus</i>			3	5					
* <i>Buddleja saligna</i>			4	3					
<i>Sarcostemma viminalis</i>			4	3					

A : *Cassine aethiopica*-*Cussonia thyrsiflora*
South East Dune Thicket

B : *Cassine aethiopica*-*Schotia afra*
Alexandria Dune Thicket

C : *Pterocelastrus tricuspidatus*-*Gonioma kamassi*
Knysna thicket

D : *Pterocelastrus tricuspidatus*- *Euclea undulata*
Kromme River Thicket

* Diagnostic species for Kaffrarian Thicket including:

1 Kaffrarian Transition Zone endemics (Cowling, 1982e);

2 southern and south western Cape endemics

shrubland community), from near Stanford by Taylor (1961 - Calvaria (= Sideroxylon)-Euclea Short Forest), from Betty's Bay by Boucher (1978 - Colpoon-Rhus scrub, Sideroxylon scrub), from the Cape Flats by Taylor (1972 - Pterocelastrus dune scrub), and from the Cape of Good Hope Nature Reserve by Taylor (1969 - Sideroxylon scrub association). Taylor (1978) gives a general account of coast scrub (dune thicket) for the Cape region and Phillips (1931) and Muir (1929) describe dune thickets from Knysna and Riversdale districts respectively.

Kaffrarian Thicket communities on clayey substrates are described from the Keiskammahoek district by Story (1952 - Acacia scrub, Fort Cox scrub, Nqhumeya scrub, Zanyokwe bush), from the Albany and Bathurst districts by Martin and Noel (1960 - Warm temperate forest scrub, Acacia karroo-Cussonia spicata alliance, particularly bush-clump savannah type), from near Grahamstown by Jessop and Jacot Guillarmod (1969 - Forest and Thicket Areas D, F, G and H), and from the Addo National Park by Archibald (1955 - Bontveld). Muir (1929) gives a general account of clay thicket in the Riversdale district and Taylor (1970b) describes a single community near Riversdale.

The mountain thicket form of Kaffrarian Thicket is restricted to arenaceous substrates of the T.M.G. and has strong Afromontane links. Phillips (1931) and Von Breitenbach (1974) describe mountain and clay thickets from the Knysna forest enclave.

I recognised four Kaffrarian Thicket communities from the study area (Table 8). The Cassine-Cussonia (Figures 23 and 37) and Cassine-Schotia communities are both dune thickets. The former is synonymous with Van der Merwe's (1976) Sideroxylon inerme forest community and occurs on deep humic sands (Fernwood form) of the coastal dunes. It is closely related to the dune thicket of the southern and south western Cape but has a richer component of subtropical shrubs. In the study area the Cassine-Cussonia community is confined to the wetter parts of the coast west of the Kromme river.

The Cassine-Schotia community is a drier dune thicket with a higher proportion of succulents, spiny shrubs and vines. It also has a number of Kaffrarian Succulent Thicket diagnostic species indicating strong links with this type. It resembles the Coastal Bush described by Archibald (1955) at Addo, and the Sundays River Scrub described by Taylor and Morris (1981) on the Algoa Bay coast. The Cassine-Schotia community occurs east of the Kromme river on deepish dune sands.



Fig. 37: Cassine-Cussonia Dune Thicket (right) on deep well-drained sand (Fernwood form) and Restio-Agathosoma Dune Fynbos (left) on shallow sand overlying gאלcrete (Mispah form). Cape St. Francis (c. 20 m).

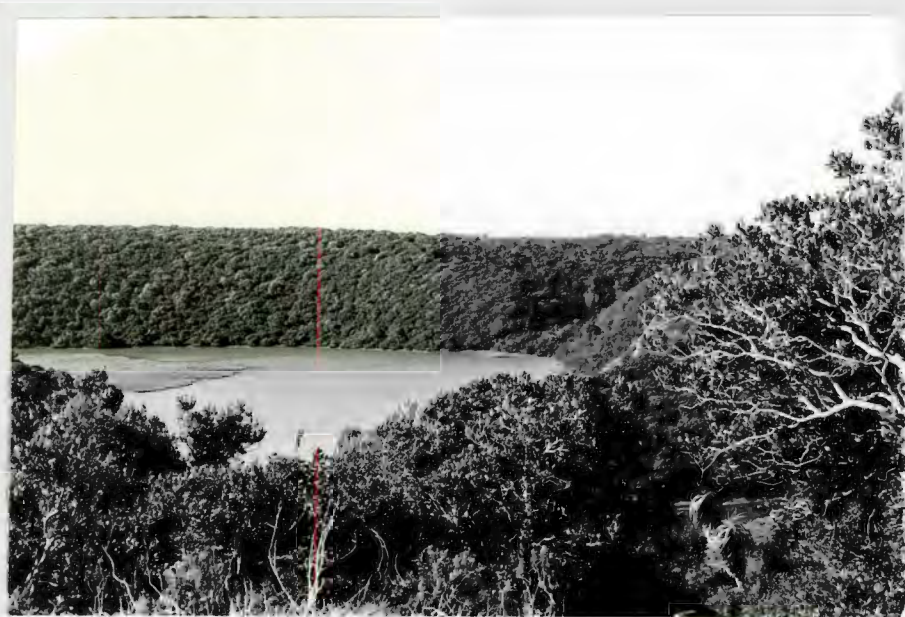


Fig. 38: Pterocelastrus Euclea Thicket in the Kromme river valley on well-drained Hutton soils (Bokkeveld shale). Dominant species are Pterocelastrus tricuspidatus, Cassine aethiopica, Euclea undulata, Aloe pluridens and Sideroxylon inerme. (c. 30 m).



Fig. 39: Kaffrarian Thicket, Euclea-Pterocelastrus community, on deep, reddish loams (Hutton form) derived from Congo limestone, Elandsberg foothills (c. 300 m). Dominant species: Polygala myrtifolia, Euclea undulata, Olea europaea, Ochna serrulata, Schotia latifolia. Kleinfontein limestone quarry near Loerie.



Fig. 40: Pterocelastrus-Gonioma Knysna Thicket on T.M.G. sandstone on colluvial talus and breccia soils. Krommellenboog between Cape St. Francis and Oyster Bay (c. 60 m).

The Pterocelastrus-Euclea community occurs on well drained clayey soils in the valleys incised into the coastal plain and also on termitaria on the interfluvies (Figures 28 and 38). Another block occurs in the foothills of the Elandsberg above the drier succulent thicket (Fig. 39). The Pterocelastrus-Gonioma community (Fig. 40) is restricted to T.M.G. sandstone and quartzites and occurs on stable scree and talus slopes, slope breccias and other rocky colluvial sites where soils are deep and stony. Under identical rainfall régimes this community is more mesic and has stronger Afromontane links than the Pterocelastrus-Euclea community. This is probably due to better infiltration afforded by the sandier soils of the former community.

More details on these Kaffrarian Thicket communities are given in Cowling (1982 a - d).

3.3.2 Kaffrarian Succulent Thicket

Kaffrarian Succulent Thicket consists of the Transitional Thicket communities where succulents contribute 20 - 30% relative cover (Fig. 36). They occur in the hot, dry river valleys from the Kei to the Gouritz (Table 3). Like the Kaffrarian Thicket they have their maximum expression in the Kaffrarian Transition Zone, particularly the Fish and Sundays river valleys. Succulents are well adapted to grow in the valley climates (1.3) where soil moisture is limiting for extended periods (Cowling and Campbell, 1982 a).

Diagnostic species include a number of regional and local character species, many of which are succulent shrubs of karroid affinity (Table 9). Phytochorological affinities are complex but Tongaland-Pondoland endemics and linking species predominate; a Karoo-Namib influence is strong (Fig. 35). Endemism is more pronounced than in Kaffrarian Thicket due to a strong representation of regional endemics of karroid affinity (Fig. 35). The Kaffrarian Transition Zone is a centre of endemism of succulent Euphorbia species (Croizat, 1965), where 14,5% of southern African species are confined (data from White *et al.*, 1941), most of which are found in Kaffrarian Succulent Thicket. Aloe, Crassula and Delosperma have numerous species in these communities and many are endemic. There are very few subtropical shrub and tree endemics (Fig. 35).

A great diversity of growth forms are found in Kaffrarian Succulent Thicket. These include leaf and stem succulent shrubs, trees and vines, arborescent rosette succulents, succulent herbs, large- and small-leaved sclerophyllous and orthophyllous shrubs, low trees and vines, grasses, forbs, annuals and geophytes (Fig. 41). Bews (1925) believes

TABLE 9. Kaffrarian Succulent Thicket communities

Community Number of relevés	A 3	B 5	C 10	Community Number of relevés	A 3	B 5	C 10
* <i>Senecio longifolius</i>	5			<i>Cassine tetragona</i>		4	3
* <i>Brachylaena ilicifolia</i>	5	1		<i>Asparagus aethiopicus</i>		3	4
<i>Helichrysum rasum</i>	5			<i>Plectranthus madagascariensis</i>		3	4
<i>Rhoicissus tridentata</i>	5		1	<i>Maerua caifra</i>		3	2
* <i>Pappea capensis</i>	5	2	1	<i>Carissa bispinosa</i>		3	2
<i>Clusia daphnoides</i>	5	2	1	<i>Cassine aethiopica</i>		2	2
<i>Polygala myrtifolia</i>	5	1		<i>Euclea undulata</i>	5	5	4
<i>Euryops euryopoides</i>	4			* <i>Capparis sepiaria</i>	5	4	4
* <i>Euryops spathaceus</i>	4			<i>Aloe ferox</i>	4	5	5
<i>Ehrharta calycina</i>	4			* <i>Crassula cultrata</i>	5	5	3
<i>Euclea racemosa</i> ssp. <i>daphnoides</i>	4			<i>Rhoiacarpus capensis</i>	4	5	3
<i>Schotia latifolia</i>	4	1	1	¹ <i>Delosperma ecklonis</i>	4	5	3
¹ <i>Senecio pyramidatus</i>		4		* <i>Azima tetracantha</i>	5	2	5
* <i>Crassula ovata</i>		4		<i>Sarcostemma viminale</i>	4	2	5
* <i>Euryops brevipapposus</i>		4	1				
¹ <i>Asparagus crassifolius</i>		4					
* <i>Bulbine alooides</i>		4					
¹ <i>Euphorbia fimbriata</i>	1	4					
¹ <i>Cussonia gamtooiensis</i>		3					
* <i>Senecio radicans</i>		3					
<i>Sansevieria</i> sp.		3	1				
* <i>Fockea edulis</i>		3	1				
<i>Aloe pluridens</i>		3					
* <i>Asparagus striatus</i>	5	5					
* <i>Euphorbia mauritanica</i>	5	5					
* <i>Crassula muscosa</i>	4	3					
* <i>Crassula perforata</i>	4	3					
<i>Hippobromus pauciflorus</i>	4	3					
* <i>Portulacaria afra</i>	4	2					
* <i>Crassula mollis</i>	4	2					
* <i>Crassula spathaceus</i>			4				
<i>Senecio angulatus</i>			4				
<i>Plumbago auriculata</i>			3				
<i>Cotyledon velutina</i>	2	1	4				
* <i>Bulbine caulescens</i>		1	3				
<i>Oxalis stellata</i>		1	3				
<i>Cynanchum ellipticum</i>			3				
<i>Stipa dregeana</i>		1	3				
* <i>Schotia afra</i>		5	4				
<i>Hypoestes verticillaris</i>		5	5				
<i>Rhus longispina</i>		4	5				
<i>Sideroxylon inerme</i>		5	4				
* <i>Asparagus africanus</i>		5	4				
<i>Scutia myrtina</i>		4	5				
<i>Rhoicissus digitata</i>		5	3				
* <i>Euphorbia grandidens</i>		4	4				

A : *Euclea undulata*-*Brachylaena ilicifolia*
Sundays River Succulent Thicket

Sideroxylon inerme-*Euphorbia grandidens*
Sundays River Succulent Thicket

B : *Schotia afra*-*Crassula ovata* sub-community

C : *Capparis sepiaria*-*Crassula spathaceus* sub-community

* Diagnostic species for Kaffrarian Succulent Thicket including:

¹ Species endemic to the Kaffrarian Transition Zone (Cowling, 1982e)



Fig. 41: Kaffrarian Succulent Thicket near the mouth of the Kabeljous River (c. 10 m). Dominant species include arborescent succulents: Euphorbia triangularis, E. grandidens, Aloe africana; sclerophyll shrubs: Euclea undulata, Sideroxylon inerme, Azima tetracantha, Rhus longispina; and vines: Rhoicissus digitata, Capparis sepiaria and Euphorbia mauritanica.



Fig. 42: Sideroxylon-Euphorbia Succulent Thicket on deep, sandy clay loams (Clovelly form). Succulents include Aloe ferox, Euphorbia grandidens, Senecio pyramidatus and Portulacaria afra. Other species are Carissa haematocarpa, Euclea undulata, Cussonia gamtoensis and Sideroxylon inerme.
Near Hankey, on road to Loerie (c. 150 m).

round on deep alluvial, bottomland soils which have not been cleared for agriculture. The Schotia-Crassula sub-community (Fig. 42) is typical of the drier, north-facing sites whereas the Capparis-Crassula sub-community occurs in moister areas. Rainfall is between 450 and 500 mm yr⁻¹.

Afromontane Forests comprise the only true forest vegetation in the Fynbos Biome. They are restricted to the southern coastal forelands and mountains, on sites where soil moisture is available throughout the year (White, 1978; McKenzie, 1978; Fig. 43). Compared to allied forests of Transkei, Natal and Transvaal, the Cape Afromontane Forests are depauperate (Von Breitenbach, 1974; White, 1978).

Afromontane Forest communities have been studied in the Grahamstown district by Dyer (1937) and Martin (1965), in the Knysna enclave by Phillips (1931) and Von Breitenbach (1974), in the Riversdale district by Muir (1929), at Grootvadersbosch by Taylor (1955), and at Cape Hangklip by Boucher (1978). McKenzie (1978) undertook a detailed phytosociological study of Afromontane Forest communities between George and the Cape Peninsula. Peninsula forest communities have been described by Campbell and Moll (1977) and McKenzie et al. (1977).

3.4.1 Knysna Afromontane Forest

The Afromontane Forest flora in South Africa is very uniform and probably consists of only a few orders within the hierarchy proposed in this paper. White (1978) recognised five local systems, three of which occur in the Cape Province. These are the Cape Province east of Knysna, the Knysna forests, and the forests west of Knysna.

The first system is centred in the southernmost spur of the Drakensberg (Winterberg and Amatole ranges) and has been studied in the Keiskammahoek district by Story (1952). Outliers occur along the Zuurberg range (Martin and Noel, 1960; Martin, 1965). These forests have a number of species not found further westwards (see White, 1978 p. 503) and are characterized by a high cover of Canthium ciliatum in the understorey (cf. Story, 1952; Acocks, 1953; pers. obs.).

Forests in the Knysna region have been studied extensively in the past (Phillips, 1931; Von Breitenbach, 1974). I include them with the forests of the south western Cape as a separate order (Knysna Afromontane Forest). Knysna forests usually have a great deal of Gonioma kamasii in the understorey whereas in south western Cape forests, Hartogia schniodes is a dominant understorey species (see Campbell and Moll, 1977; McKenzie et al., 1977; Boucher, 1978; McKenzie, 1978).



Fig. 43: Afromontane forest on the Elandsberg on a convex slope (colluvium) at the line of contact between T.M.G. quartzite and Congo phyllite and quartzite. Road between Otterford and Kleinfontein (c. 400 m).



Fig. 44: Afromontane Forest, Rapanea-Ocotea community, on deep colluvial soil (Oakleaf form) in the Elandsberg. Dominant species: Ocotea bullata, Curtisia dentata, Alsophilla capensis, Trichoclados crinitus, Rapanea melanophloeos. Loerie "Stinkwood" forest (c. 500 m).

I recognised two Knysna Afromontane Forest communities in the study area: Rapanea-Canthium community and the Rapanea-Ocotea community (Table 10). Both occur in colluvial basins or valley fills in the Elandsberg mountains (Figures 43 and 44). The former is found in isolated pockets at the junction of the T.M.G. and Cango quartzite where the rainfall is between 700 and 900 mm yr⁻¹. The latter is restricted to a small basin above the Loerie forest station which receives a rainfall in excess of 1 000 mm yr⁻¹. Soils are deep with loamy topsoils which grade into sandy clay loam subsoils (Oakleaf form). They receive runoff throughout the year and have a good water retaining capacity.

4.0 DISCUSSION

4.1 Soil nutrients and shrubland types

Specht and Moll (1982) include the Humansdorp region in the mediterranean climate zone of South Africa (see also Di Castri, 1980; 1.3). The dominant vegetation classes in the study^{area} (Cape Fynbos Shrublands and Cape Transitional Small-leaved Shrublands) are typical of the south western Cape which does enjoy a true mediterranean climate. Below I examine the shrublands of the Humansdorp study area in terms of current concepts of mediterranean shrublands (Specht, 1979; Di Castri, 1980; Specht and Moll, 1982).

Specht and Moll (1982) make a fundamental distinction between South African mediterranean shrublands (with open-scrub overstorey of evergreen sclerophyllous shrubs over an understorey of seasonal grasses and herbs) on base-rich soils, and heathlands (with evergreen sclerophyllous strata of Proteaceae, Ericaceae and Restionaceae) on nutrient-poor soils. A third category of shrublands is confined to calcium-rich soils where a stunted overstorey of evergreen sclerophyllous trees or shrubs occurs over a ground stratum showing a gradation from seasonal grasses and herbs to evergreen hemicryptophytes (restioids and cyperoids) (Specht and Moll, 1980).

Table 11 shows the relations of Humansdorp shrublands to the soil sites defined by Specht (in Specht and Moll, 1982; Campbell, 1982 a).

Thicket grows on base-rich and calcium-rich soils. The structure and composition of the thicket on the different soil suites is very similar (Cowling and Moll, 1982; Table 8). They deviate from the structural characterization given for South African mediterranean

TABLE 11. Correspondence of vegetation types (shrublands only) in the Humansdorp region to base-rich, nutrient-poor and calcium-rich soil suites defined by Specht (pers. comm.; Specht and Moll, 1982)

Base-rich soils	Nutrient-poor soils	Calcium-rich soils
Kaffrarian Thicket ¹	Mountain Fynbos ¹	South Coast Dune Fynbos ⁴
Kaffrarian Thicket ²	Grassy Fynbos ¹	Kaffrarian Thicket ⁴
Kaffrarian Succulent Thicket ²	Grassy Fynbos ³	
Kaffrarian Succulent Thicket ³	South Coast Renosterveld ²	
South Coast Renosterveld ²	South Coast Renosterveld ³	
South Coast Renosterveld ³		

¹T.M.G. sandstone and quartzites

²Bokkeveld Shale

³Enon deposits

⁴Recent sands

shrublands on base-rich soils by Specht and Moll (1982; Table 5) in that they are closed (never savannoid) and have a sparse understorey of shade tolerant grasses and herbs. South Coast Renosterveld occurs on soils which are marginally base-rich or nutrient-poor (Table 11, Fig. 8). Specht and Moll (1982) include renosterveld as a mediterranean shrubland on base-rich soils which has been derived recently from "an open-scrub formation, dominated by Olea africana and Sideroxylon inerme". The latter is regarded as the "true-mediterranean shrubland analogous to matorral, maquis, chaparral and mallee of other lands with mediterranean-type climate (Boucher and Moll, 1980; Di Castri, 1980). I have argued (3.2.1) that South Coast Renosterveld is derived from a grassland (or open grassy small-leaved shrubland) and that the "Olea-Sideroxylon open-scrub" is restricted to special edaphic sites and represents a westward penetration of subtropical thicket. South Coast Renosterveld does have the understorey characteristics of shrublands (sensu Specht and Moll, 1982) but does not have any clear analogue in other mediterranean lands. Axelrod (1978) argues a post-glacial origin for California coastal sage and a recent spread induced by man's disturbances to the landscape (see 2.3.1). Westman (1981; pers. comm.) sees very little structural similarity between renosterveld and coastal sage scrub.

Shrublands on nutrient-poor soils or heathlands (sensu Specht, 1979; Specht and Moll, 1982) include S.E. Mountain Fynbos and Grassy Fynbos. Bond (1981) and Campbell et al. (1981) restrict the use of heathland to communities dominated by ericaceous shrubs whereas Specht's concept has a much wider applicability. Grassy Fynbos is anomolous since it has an understorey that is often dominated by seasonal grasses (Fig. 10) even when the overstorey is composed of ericaceous shrubs. Grassy Fynbos soils are slightly more fertile than Mountain Fynbos soils (Fig. 8; 3.1.2).

Dune Fynbos on calcium-rich soils shows both heathland and shrubland characteristics (Fig. 10). These transitional features are not so much reflected in the structure of the understorey (cf. Specht and Moll, 1982) but in intermingling and mosaic patterns of shrubland (large-leaved subtropical shrubs) and heathland (small-leaved fynbos shrubs) overstoreys on deep, well drained sands. Dune Fynbos on shallow sands overlying calcrete conforms to Specht's (1979) heathland concept.

Table 12 shows the correlations between some soil variables and biogeographical phyto-chorological groups characteristic of shrubland types in the study area. Cape endemics are characteristic of Mountain and Grassy Fynbos (Cowling, 1982e; Fig. 9) and show a highly significant negative relationship with soil depth, litter, organic carbon and all

TABLE 12. Correlation between soil variables and dominant phytocorological groups in the Humansdorp study area. Data from 97 relevés. Sample distribution as in Fig. 8 and including two samples from alluvium (Kaffrarian Succulent Thicket) and two samples from Congo limestone and phyllite (Kaffrarian Thicket)

	Soil depth	Rock cover	Litter	% sand	pH	S-value	Available calcium	Organic carbon	Total nitrogen	Available phosphorus
Cape endemics	----	++++	----	++++	----	----	----	----	----	----
Cape-Afromontane linking	--		----			----	----	----	----	----
Cape-Karoo-Namib linking	----	++++	----		-	--	-			
Tongaland-Pondoland endemics	++++	---	++++	---	++++	++++	++++	++++	++++	++++
Cape-Tongaland-Pondoland linking	+++	-		+++	++++	++	++++			+
<hr/>										
- +	:	<u>P</u>	<	,05						
-- ++	:	<u>P</u>	<	,02						
--- +++	:	<u>P</u>	<	,01						
---- ++++	:	<u>P</u>	<	,001						

major nutrients; they show significant positive relationships with percentage sand and rock cover. In general, a high incidence of fynbos elements is associated with shallow, rocky, infertile, sandy soils.

Cape-Afromontane linking species are typical of moist renosterveld (Themeda-Cliffortia community) and to a lesser extent, Grassy Fynbos (Cowling, 1982e; Fig. 9).

Correlations with soil variables are similar to Cape endemics except there are no significant correlations with percentage sand, pH and rock cover. Cape-Karoo-Namib linking species are characteristic of drier renosterveld communities (Elytropappus-Eustachys and Elytropappus-Relhania) (Cowling, 1982e). They show very weak relationships with soil nutrients indicating the intermediate fertility status of renosterveld soils in relation to the full spectrum of soils sampled. The highly significant positive correlation between the percentage of Cape-Karoo-Namib linking species and rock cover is a result of the concentration of these species in the Elytropappus-Eustachys community on stony soils derived from Enon conglomerate.

The Tongaland-Pondoland endemics typify thicket communities (Cowling, 1982e; Fig. 35) and show relationships with soil variables that are exactly the inverse of the Cape endemics (Table 12). Soils are deep, base-rich, sandy loams to sandy clays.

Cape-Tongaland-Pondoland linking species are commonly found in Dune Fynbos but also occur in renosterveld (Cowling, in press; Fig. 9). They show highly significant positive correlations with available calcium and pH (calcium-rich soils sensu Specht and Moll (1982) and weaker positive relationships with percentage sand, S-value and available phosphorus (Table 12).

Soil nutrients are of value in differentiating amongst classes and orders of shrublands in the study area. There is a fertility gradient ranging from Mountain Fynbos soils (least fertile), through Grassy Fynbos and South Coast Renosterveld, to thicket soils. Dune Fynbos occurs on calcareous sands with markedly different chemical characteristics to other fynbos soils. The only soil factor common to all fynbos shrublands in the study area is a sandy texture.

Specht and Moll's (1982) plant formations (shrubland types) characteristic of base-rich, nutrient-poor and calcium-rich soils are of limited value when applied to shrublands in the Humansdorp study area. Specifically the marginal status of renosterveld soils is obscured. Moreover many shrublands on true base-rich soils are not Cape mediterranean communities but subtropical thicket.

4.2 The role of soil moisture

Soil moisture plays a critical role in the distribution of phytocoenoses at all levels of the hierarchy. Most thicket communities and forest are confined to deep, well drained soils with good water holding capacity. Succulent thicket, thicket and forest can be ranged along a gradient of decreasing soil moisture deficit (Cowling and Campbell, 1982b).

Within the Cape Fynbos Shrublands and Transitional Small-leaved Shrublands there are edaphic grasslands and restioid grasslands on hardpan soils with seasonably high watertables. Well drained shallow or stony soils support small-leaved or proteoid shrublands on all substrate types. On deep, excessively drained dune sands, fynbos is successional to thicket whereas similarly-structured sands derived from T.M.G. sandstone support fynbos as a climax.

Soil structure, moisture and nutrient status form a complex group of interrelated factors that determine vegetation composition and structure. These factors are explored more fully in Cowling (1982 a-d).

4.3 Tension zones and phytochorological complexity

The Cape mediterranean climate zone is not isolated from the summer rainfall region but grades into it along the southern and south eastern coastal forelands, thus facilitating the penetration of subtropical elements into the Fynbos Biome. The hot, dry valleys of the Fish, Sundays, Gamtoos and Gouritz rivers provide a coastwards migratory pathway for karroid elements from the dry intermontane valleys and upland basins to the north. Furthermore in the south eastern and southern Cape, where there is a warm temperate climate at the coast, Afromontane species are widespread at low altitudes.

The chorological complexity of the south eastern Cape is due to the transitional nature of the climate and complex topographical, geological and soil patterns (Gibbs Russel and Robinson, 1981). The whole region comprises a huge tension zone where major phytochoria converge. In the south eastern and southern Cape this complexity is best expressed on the relatively fertile soils of the coastal forelands. Subtropical thickets of the river valleys have admixtures of Karoo-Namib taxa; in more mesic areas there is a strong Afromontane influence. South Coast Renosterveld has species contributed from the Cape, Karoo-Namib, Afromontane and Tongaland-Pondoland phytochoria. On the

lower slopes and planed surfaces of the Cape Fold Mountains, there is Grassy Fynbos which links Mountain Fynbos and the Afromontane grasslands of the eastern Cape (Dohne Sourveld (41)). There are patterns of intermingling of elements (e.g. Sub-tropical grasses in Grassy Fynbos and South Coast Renosterveld) and interdigitation of communities (e.g. thicket on special edaphic sites in Grassy Fynbos and South Coast Renosterveld).

Mountain fynbos, of wholly Cape affinity, occurs on mountain "islands" within the "sea" of chorological complexity that comprises the vegetation on the coastal forelands in the south eastern and southern Cape. Towards the east this Mountain Fynbos island is pinched into a narrow peninsula on the upper slopes of the Elandsberg and Groot Winterhoek mountains.

A study of the chorological complexity and endemism of these vegetation types, together with a knowledge of the ecological relations of the modern taxa that contribute to them, provides the basis for hypotheses on the historical biogeography of the area. I explore this elsewhere (Cowling, 1982e).

4.4 Conservation

A fundamental aim of the Fynbos Biome project is the stimulation of research focussing on the management and conservation of Biome communities (Kruger, 1978). It is not my intention to digress at length on the conservation status of each community recognised in this study. Rather, I wish to highlight situations where unique components will be lost unless immediate action is taken.

Much attention has been given to the conservation of Mountain Fynbos and Kruger (1977) has proposed a series of mountain reserves within recognised biogeographical centres. Much of the area of Mountain Fynbos is controlled by the Department of Water Affairs, Forestry and Environmental Conservation and although some of this land could be afforested in the future, theoretically the situation is good as the department explicitly provides for conservation in these areas (Kruger, 1977).

In direct contrast the conservation status of the lowland regions in the Biome is critical (Taylor, 1978; Boucher and Moll, 1980). Coastal Renosterbosveld (46) now covers only 9% of its former extent, having been largely replaced by agricultural crops (Taylor, 1978). About 1% of its former total area is conserved (Edwards, 1974).

The conservation status of Coastal Fynbos (47) is equally dismal with only 2,1% of its former total extent conserved (Edwards, 1974).

Most of the study area is on the lowlands where land is privately owned and not subject to state control. Grassy Fynbos is maintained in a semi-natural state for rangeland. Since this form of land-use is likely to persist over much of its area, the conservation status of these communities is not regarded as critical. The current fire régime in Grassy Fynbos has resulted in the local elimination of a seed regenerating species (Fig. 14). Grassy Fynbos in the south eastern Cape is conserved in the Kouga, Groendal and Suurberg wilderness areas (Kruger, 1977).

South Coast Renosterveld communities in the study area are severely threatened as they occur on arable soils. Their conservation invokes the problem of the withdrawal of high potential land from agriculture. The present trend of ploughing up natural veld in order to establish artificial pastures and cereal crops is proceeding at an alarming rate. There are great economic incentives to replace degraded renosterveld with more productive agricultural crops. Renosterveld communities are scientifically important as they reflect to the fullest the biogeographical complexity of the south eastern Cape vegetation. Immediate steps should be taken to ensure adequate conservation. I propose that a reserve is established to incorporate the hilly country and parts of the adjacent coastal plain on the southern side of the Gamtoos valley. This area would include Elytropappus-Relhania Renosterveld and Euclea-Brachylaena Succulent Thicket on Bokkeveld shale and Elytropappus-Eustachys Renosterveld and Themeda-Passerina Grassy Fynbos on Enon conglomerate. The topography is such that most of the area is unsuitable for crop husbandry.

Attention has already been drawn to the critical state of dune fynbos and thicket communities in the study area (Cowling, 1980). Dune coasts are dynamic, fragile ecosystems, extremely vulnerable to disturbance and quickly destroyed by human irresponsibility (Heydorn and Tinley, 1980). The dune communities are certainly the most threatened in the region. A number of factors, including indiscriminate and poorly planned resort development and poor agricultural management have contributed to the destruction of natural vegetation, the thickening up and spread of alien Acacia spp. and the reactivation of stable dunes.

The only two provincial nature reserves in the study area are located on the coast. However, together they cover less than 100 ha and provide inadequate conservation

for the region's flora and fauna (Cowling, 1980). As an absolute minimum to meet the conservation requirements of the dune communities, the present reserve at Cape St. Francis should be extended to include at least 150 ha of indigenous vegetation (cf. Heydorn and Tinley, 1980).

Succulent thicket and thicket occurs mainly along water courses and in the steeply dissected country of the Gamtoos valley. Some attempts are being made to clear the thicket in the latter area but most of the land is non-arable. The immediate purchase of land for conservation is not a priority. Afromontane Forest occurs on state-controlled land and is conserved by the Department of Water Affairs, Forestry and Environmental Conservation.

REFERENCES

- Acoccks, J.P.H., 1953. Veld types of South Africa. Mem. Bot. Surv. S. Afr. 28.
- Acoccks, J.P.H., 1979. The flora that matched the fauna. Bothalia 12 : 673 - 709.
- Adamson, R.S., 1948. Some geographical aspects of the Cape flora. Trans. R. Soc. S. Afr. 31 : 437 - 464.
- Anon., 1942. Weather on the coasts of southern Africa. Part 3. Union of South Africa from Mossel Bay to East London. Pretoria: Government Printer.
- Archibald, E.E.A., 1955. An ecological survey of the Addo Elephant National Park. Jl. S. Afr. Bot. 20 : 137 - 154.
- Aucamp, A.J., & Barnard, H.H., 1980. Die ontplooiing van die veekundpotensiaal van die droë gras-bosgemeenskappe van die Oos-Kaap. Proc. Grassld. Soc. sth. Afr. 15 : 137 - 140.
- Austin, M.P., 1977. Use of ordination and other multivariate descriptive methods to study succession. Vegetatio 35 : 165 - 175.
- Aweto, A.O., 1981. Organic matter build-up in fallow soil in part of south-western Nigeria and its effects on soil properties. J. Biogeogr. 8 : 67 - 74.
- Axelrod, D.I., 1978. Origin of coastal sage vegetation, Alta and Baja California. Amer. J. Bot. 65 : 1117 - 1131.
- Bagshawe-Smith, L., 1937. Rhenosterbush in the district of Albany. S. Afr. J. Sci. 33 : 335.
- Barkman, J.J., Moravec, J. & Rauschert, S., 1976. Code of phytosociological nomenclature. Vegetatio 32 : 131 - 185.
- Basset, P.A., 1978. The vegetation of a Camargue pasture. J. Ecol. 66 : 803 - 827.
- Bews, J.W., 1917. The plant succession in the thorn veld. S. Afr. J. Sci. 14 : 153 - 172.
- Bews, J.W., 1925. Plant forms and their evolution in South Africa. London : Longmans.
- Bond, W.J., 1980a. Periodicity in fynbos of the non-seasonal rainfall belt. Jl. S. Afr. Bot. 46 : 343 - 354.
- Bond, W.J., 1980b. Fire and senescent fynbos in the Swartberg, Southern Cape. S. Afr. For. J. 114 : 68 - 71.
- Bond, W.J., 1981. Vegetation gradients in the southern Cape mountains. M.Sc. thesis, University of Cape Town (unpublished).
- Botanical Research Institute (B.R.I.), not dated. The standardization of syntaxonomic nomenclature. Pretoria : B.R.I. (unpublished).

- Botha, C.G., 1923. The dispersion of the stock farmer in the Cape Colony in the eighteenth century. S. Afr. J. Sci. 20 : 574 - 580.
- Boucher, C., 1978. Cape Hangklip area. 11. The vegetation. Bothalia 12 : 455 - 497.
- Boucher, C., 1980. Notes on the use of the term "Renosterveld". Bothalia 13 : 237.
- Boucher, C., 1982. Floristic and structural features of the coastal foreland vegetation south of the Berg river, western Cape Province, South Africa.
Proceedings of the 10th AETFAT Congress, Pretoria (in press).
- Boucher, C. & Jarman, M.L., 1977. The vegetation of the Langebaan area, South Africa. Trans. R. Soc. S. Afr. 42 : 241 - 272.
- Boucher, C. & Moll, E.J., 1980. South African mediterranean shrublands.
In F. di Castri, D.W. Goodall & R.L. Specht, eds. Mediterranean-type shrublands. Amsterdam : Elsevier.
- Brady, N.C., 1974. The nature and property of soils 8th Edn. New York : Macmillan.
- Butzer, K.W. & Helgren, D.M., 1972. Late Cainozoic evolution of the Cape coast between Knysna and Cape St. Francis, South Africa. Quart. Res. 2 : 143 - 169.
- Campbell, B.M., 1978. Similarity coefficients for classifying relevés. Vegetatio 37 : 101 - 109.
- Campbell, B.M., 1982a. Plant environment of the mountains of the Fynbos Biome. Bothalia (in press).
- Campbell, B.M., 1982b. Vegetation classification in a floristically complex zone: the Cape Floristic Region (in prep.).
- Campbell, B.M. & Moll, E.J., 1977. The forest communities of Table Mountain, South Africa. Vegetatio 34 : 105 - 115.
- Campbell, B.M., Cowling R.M., Bond, W.J. & Kruger, F.J., 1981.
Structural characterization of vegetation in the Fynbos Biome.
South African National Scientific Programmes Report No. 53.
Pretoria: C.S.I.R.
- Campbell, J., 1815. Travels in South Africa. London: Black, Parry and Co.
- Charley, J.C. & West, N.E., 1975. Plant induced chemical patterns in some shrub dominated semi-desert ecosystems of Utah. J. Ecol. 63 : 945 - 963.

- Clements, F.E., 1916. Plant succession. Washington: Carnegie Inst. Publ. No. 242.
- Connel, J.H. & Slatyer, R.O., 1977. Mechanism of succession in natural communities and their role in community stability and organisation. Amer. Nat. 111: 1119 - 1144.
- Cowling, R.M., 1980. The coastal dune ecosystems of the Humansdorp district - a plea for their conservation. East. Cape Natur. 70 : 25 - 28.
- Cowling, R.M., 1982a. Vegetation of the Humansdorp region, south eastern Cape. 1. Communities on Recent dune sands (in prep.).
- Cowling, R.M., 1982b. Vegetation of the Humansdorp region, south eastern Cape. 2. Communities on the Table Mountain Group (in prep.).
- Cowling, R.M., 1982c. Vegetation of the Humansdorp region, south eastern Cape. 3. Communities on Bokkeveld shale and Enon conglomerate (in prep.).
- Cowling, R.M., 1982d. Vegetation of the Humansdorp region, south eastern Cape. 4. Communities of the lower Gamtoos River valley (in prep.).
- Cowling, R.M., 1982e. Phytochorology and vegetation history in the south eastern Cape, South Africa (in prep.).
- Cowling, R.M., 1982f. Diversity relations in fynbos and non-fynbos communities in the south eastern Cape, South Africa (in prep.).
- Cowling, R.M., 1982g. The occurrence of C3 and C4 grasses in fynbos and allied shrublands in the south eastern Cape, South Africa (in prep.).
- Cowling, R.M. & Campbell, B.M., 1982a. Defining leaf texture categories in the Fynbos Biome. Jl. S. Afr. Bot. (in press).
- Cowling, R.M. & Campbell, B.M., 1982b. A comparison of fynbos and non-fynbos coenoclines in the lower Gamtoos River valley, south eastern Cape, South Africa (in prep.).
- Cowling, R.M. & Moll, E.J., 1982. Growth form distribution in fynbos and non-fynbos communities in the south eastern Cape, South Africa (in prep.).
- Croizat, L., 1965. An introduction to the subgeneric classification of Euphorbia L. with stress on the South African and Malagasy species. Webbia 20 : 573 - 706.
- Date, M.B. & Webb, L.J., 1975. Numerical methods for the establishment of associations. Vegetatio 30 : 77 - 87.

- Daniels, R.E., 1978. Floristic analysis of British Mires and Mire communities. J. Ecol. 66 : 773 - 803.
- Deacon, H.J., 1979. Excavations at Boomplaas Cave : a sequence through the Upper Pleistocene and Holocene in South Africa. World Archaeology 10 : 241 - 257.
- Deacon, H.J., 1982. The comparative evolution of mediterranean-type ecosystems: a southern perspective. In F.J. Kruger, D.T. Mitchell and J.U.M. Jarvis, eds. Mediterranean-type ecosystems. The role of nutrients. Berlin-Heidelberg-New York: Springer (in press).
- Deacon, H.J. & Brooker, M., 1976. The Holocene and Upper Pleistocene sequence in the southern Cape. Ann. S. Afr. Mus. 71 : 203 - 214.
- Di Castri, F., 1980. Mediterranean-type shrublands of the world. In F. di Castri, D.W. Goodall & R.L. Specht, eds. Mediterranean-type shrublands. Amsterdam : Elsevier.
- Drury, W.H. & Nisbet, I.C.T., 1973. Succession. J. Arnold Arboretum 54 : 331 - 368.
- Du Toit, A.L., 1966. The geology of South Africa. 3rd edn. Edinburgh and London : Oliver and Boyd.
- Du Toit, P.F., 1972. Acacia karroo intrusion: the effect of burning and sparing. Proc. Grassld. Soc. sth. Afr. 7 : 429 - 430.
- Du Toit, R. & Du Toit, E., 1938. Rhenosterbush as a weed. Farming in South Africa 13: 429 - 430.
- Dyer, R.A., 1937. The vegetation of the divisions of Albany and Bathurst. Mem. Bot. Surv. S. Afr. 17.
- Edwards, D., 1967. A plant ecology survey of the Tugela River Basin. Mem. Bot. Surv. S. Afr. 36.
- Edwards, D., 1974. Survey to determine the adequacy of existing conserved areas in relation to vegetation types. A preliminary report. Koedoe 17 : 3 - 38.
- Egler, F.E., 1954. Vegetation science concepts. 1. Initial floristic composition - a factor in old field development. Vegetatio 4 : 412 - 417.
- Fanshawe, D.B., 1968. The vegetation of Zambian termitaria. Kirkia 6 : 169 - 179.

- Fourcade, H.G., 1941. Check-list of the flowering plants of the divisions of George, Knysna, Humansdorp and Uniondale. Mem. Bot. Surv. S. Afr. 20.
- Garland, G.C., 1979. Assymetry in Drakensberg valleys: an alternative point of view. S. Afr. J. Sci. 75 : 138 - 139.
- Gauch, H.G. & Whittaker, R.H., 1981. Hierarchical classification of community data. J. Ecol. 69 : 537 - 557.
- Gerryts, E.J., 1949. Humansdorp se groei and bloei. Humansdorp: Biblioteek Pers.
- Gibbs Russel, G.E. & Robinson, E.R., 1981. Phytogeography and speciation in the vegetation of the eastern Cape. Bothalia 13 : 467 - 472.
- Gleason, H.A., 1926. The individualistic concept of the plant association. Bull. Torrey Bot. Club. 53 : 7 - 26.
- Glenn Lewin, D.C., 1980. The individualistic nature of plant community development. Vegetatio 43 : 141 - 146.
- Glyphis, J.P., Moll, E.J. & Campbell, B.M., 1978. Phytosociological studies on Table Mountain, South Africa: 1. The back Table. Jl. S. Afr. Bot. 44 : 281 - 289.
- Goldblatt, P., 1978. An analysis of the flora of southern Africa: its characteristics, relationships and origins. Ann. Missouri Bot. Gard. 65 : 369 - 436.
- Goodall, D.W., 1977. Dynamic changes in ecosystems and their study: the roles of induction and deduction. J. Environ. Mgmt. 5 : 309 - 317.
- Granger, J.E. & Schulze, R.E., 1977. Incoming solar radiation patterns and vegetation response : examples from the Natal Drakensberg. Vegetatio 35 : 47 - 54.
- Grobler, P.J. & Marais, J., 1967. Die plantgroei van die Nasionale Bontebokpark, Swellendam. Koedoe 10 : 132 - 148.
- Hall, T.D., 1934. South African pastures : retrospective and prospective. S. Afr. J. Sci. 31 : 59 - 97.
- Hall, J.B. & Swaine, M.D., 1976. Classification and ecology of closed-canopy forest in Ghana. J. Ecol. 64 : 913 - 915.
- Haughton, S.H., Frommurze, H.F. & Visser, D.J.L., 1937. The geology of portions of the coastal belt near the Gamtoos valley, Cape Province. Geological Survey Report No. 151. Pretoria: Government Printer.

- Heddle, E.M. & Specht, R.L., 1975. Dark Island Heath (Ninety-Mile Plain, South Australia). VIII. The effect of fertilizers on composition and growth, 1950 - 1972. Austr. J. Bot. 23 : 151 - 164.
- Helgren, D.M. & Butzer, K.W., 1977. Palaeosols of the southern Cape coast, South Africa. Implications for laterite definition, genesis and age. Geogr. Rev. 67 : 430 - 445.
- Heydorn, A.E.F. & Tinley, K.L., 1980. Estuaries of the Cape. Part 1. Synopsis of the Cape coast : natural features, dynamics and utilization. C.S.I.R. Research Report 380. Pretoria: C.S.I.R.
- Hill, M.O., 1973. Reciprocal averaging : an eigenvector method of ordination. J. Ecol. 61 : 237 - 249.
- Hill, M.O., 1979. TWINSPAN - A FORTRAN programme for arranging multivariate data in ordered two-way tables by classification of individuals and attributes. Ithaca, New York : Section of Ecology and Systematics, Cornell University.
- Hill, M.O., Bunce, R.G.H. & Shaw, M.W., 1975. Indicator species analysis, a divisive polythetic method of classification and its application to a survey of native pinewoods in Scotland. J. Ecol. 63 : 597 - 613.
- Holland, P.G. & Steyn, D.G., 1975. Vegetational responses to latitudinal variations in slope angle and aspect. J. Biogeogr. 2 : 179 - 183.
- Holland, P.G., Steyn, D.G. & Fuggle, R.F., 1977. Habitat occupation by Aloe Ferox Mill. (Liliaceae) in relation to topographic variations in direct beam solar radiation income. J. Biogeogr. 4 : 61 - 72.
- Holling, C.S., 1973. Resilience and stability of ecological systems. Ann. Rev. Ecol. Syst. 4 : 1 - 23.
- Horn, H.S., 1974. The ecology of secondary succession. Ann. Rev. Ecol. Syst. 5 : 25 - 37.
- Jackson, S.P. & Tyson, P.D., 1971. Aspects of weather and climate over Southern Africa. Environmental Studies Occasional Papers 6 : 1 - 11.
- Jessop, J.P. & Jacot Guillarmod, A., 1967. The vegetation of the Thomas Baines Nature Reserve. Jl. S. Afr. Bot. 35 : 367 - 392.
- Jordaan, P.G., 1964. Plantegroei van die distrikte Bredasdorp en Caledon. Tydskrif van Wetenskap en Kuns, Nuwe Reeks 6 : 47 - 58.

- Keet, D.J.M., 1936. Report on driftsands in South Africa. Forestry Department Bulletin 172.
- Kershaw, K.A., 1973. Quantitative and dynamic ecology. 2nd edn. London. Edward Arnold.
- Killick, D.J.B., 1963. An account of the plant ecology of the Cathedral Peak area of the Natal Drakensberg. Mem. Bot. Surv. S. Afr. 34.
- Killick, D.J.B., 1979. African mountain heathlands. In R.L. Specht, ed., Heathlands of the World. A. Descriptive Studies. Amsterdam : Elsevier.
- King, L.C., 1972. The coastal plain of southern Africa. Its form, deposits and development. Z. Geomorph N.F. 16 : 239 - 251.
- King, L.C., 1978. The geomorphology of central and southern Africa. In M.J.A. Werger, ed., Biogeography and ecology of southern Africa. The Hague : Junk.
- Klein, R.G., 1974. Environment and subsistence of prehistoric man in the southern Cape Province, South Africa. World Archeology 5 : 249 - 284.
- Klein, R.G., 1977. The ecology of early man in southern Africa. Science 197 : 115 - 126.
- Komarkova, V., 1980. Classification and ordination in the Indian Peaks area, Colorado Rocky Mountains. Vegetatio 42 : 149 - 163.
- Kruger, F.J., 1974. The physiography and plant communities of the Jakkalsrivier Catchment. M.Sc. thesis, University of Stellenbosch (unpublished).
- Kruger, F.J., 1977. Ecological reserves in the Cape Fynbos : towards a strategy for conservation. S. Afr. J. Sci. 73 : 81 - 85.
- Kruger, F.J., 1978. A description of the Fynbos Biome Project. South African National Scientific Programmes Report No. 28. Pretoria : C.S.I.R.
- Kruger, F.J., 1979. South African Heathlands. In R.L. Specht, ed., Heathlands of the World. A. Descriptive Studies. Amsterdam : Elsevier.
- Kruger, F.J. & Taylor, H.C., 1979. Plant species diversity in the Cape fynbos : gamma and delta diversity. Vegetatio 41 : 85 - 93.
- Laidler, D., Moll, E.J., Campbell, B.M. & Glyphis, J., 1978. Phytosociological studies on Table Mountain, South Africa. 2. The front Table. Jl. S. Afr. Bot. 44 : 291 - 295.

- Lamprechts, J.J.N., 1979. Geology, geomorphology and soils. In J. Day, W.R. Siegfried, G.N. Louw & M.L. Jarman, eds., Fynbos ecology : a preliminary synthesis. South African National Programmes Report No. 40. Pretoria : C.S.I.R.
- Lee, K.E. & Wood, T.G., 1971. Termites and soils. London : Academic Press.
- Levyns, M.R., 1926. A preliminary note on the rhenosterbush and the germination of its seed. Trans. R. Soc. S. Afr. 14 : 383 - 388.
- Levyns, M.R., 1927. A revision of Elytropappus. Jl. S. Afr. Bot. 1 : 89 - 103.
- Levyns, M.R., 1935a. Germination in some South African seeds. Jl. S. Afr. Bot. 1 : 161 - 170.
- Levyns, M.R., 1935b. Veld burning experiments at Oakdale, Riversdale. Trans. R. Soc. S. Afr. 23 : 231 - 243.
- Levyns, M.R., 1956. Notes on the biology and distribution of the rhenoster bush. S. Afr. J. Sci. 52 : 141 - 143.
- Lichtenstein, H., 1812. Travels in southern Africa. Vol. 1. London : Henry Colburn.
- Liebenberg, L.B.D., 1945. Veld management and soil utilization in the south east Cape Province. Farming in South Africa 20 : 617 - 628.
- Linder, H.P., 1982. The historical biogeography of the Disinae (Orchidaceae) in Africa (unpublished Ms.)
- Linder, H.P. & Campbell, B.M., 1979. Towards a structural-functional classification of fynbos : a comparison of methods. Bothalia 12 : 723 - 729.
- Louw, W.J., 1976. Mesoclimate of the Port Elizabeth-Uitenhage metropolitan area. Pretoria Weather Bureau Technical Paper No. 4. Pretoria : Government Printer.
- MacVicar, C.N., Loxton, R.F., Lamprechts, J.J.N., Le Roux, J., De Villiers, J.J., Verster, E., Merryweather, F.R., Van Rooyen, T.H. & Von Harmse, H.J., 1977. Soil classification. A binomial system for South Africa. Pretoria : Department of Agricultural Technical Services.
- Marloth, R., 1923. Observations on the Cape Flora : its distribution on the line of contact between the south-western districts and the Karoo. S. Afr. J. Nat. Hist. 4 : 335 - 344.
- Martin, A.R.H., 1960. The ecology of Groenvlei, a South African fen. 1. The primary communities. J. Ecol. 48 : 55 - 71.

Martin, A.R.H., 1965. Plant ecology of the Grahamstown Nature Reserve: 1.
Primary communities and plant succession. Jl. S. Afr. Bot. 31 : 1 - 54.

Martin, A.R.H., 1966. The plant ecology of the Grahamstown Nature Reserve: 2.
Some effects of burning. Jl. S. Afr. Bot. 32 : 1 - 39.

Martin, A.R.H. & Noel, A.R.A., 1960. The flora of Albany and Bathurst.
Grahamstown : Rhodes University.

McKenzie, B., 1978. A quantitative and qualitative study of the indigenous forests of the south-western Cape. M.Sc thesis, University of Cape Town (unpublished).

McKenzie, B., Moll, E.J. & Campbell, B.M., 1977. A phytosociological study of Orange Kloof, Table Mountain, South Africa. Vegetatio 34 : 41 - 53.

Milewski, A.V. & Esterhuysen, E., 1977. Habitat of Restionaceae endemic to western Cape coastal flats. Jl. S. Afr. Bot. 44 : 55 - 65.

Moll, E.J. & White, F., 1978. The Indian Ocean Coastal Belt. In M.J.A. Werger, ed., Biogeography and ecology of southern Africa. The Hague : Junk.

Mueller-Dombois, D. & Ellenberg, H., 1974. Aims and methods of vegetation ecology. New York : Wiley.

Muir, J., 1929. The vegetation of the Riversdale area. Mem. Bot. Surv. S. Afr. 13.

Nagel, J.F., 1962. Fog precipitation measurements on Africa's south-west coast. Notos 11 : 51 - 60.

Noble, I.R. & Slatyer, R.O., 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbance. Vegetatio 43 : 5 - 21.

Odum, E.P., 1969. The strategy of ecosystem development. Science 164 : 267 - 270.

Okali, D.U.U., Hall, J.B. & Lawson, G.W., 1973. Root distribution under a thicket clump on the Accra Plains, Ghana: its relevance to clump localization and water relations. J. Ecol. 61 : 439 - 454.

Olivier, M.C., 1977. A systematic check list of the spermatophyta of the Baakens River Valley, Port Elizabeth. Jl. S. Afr. Bot. 43 : 145 - 159.

Olivier, M.C., 1979. Notes on the vegetation of the Sardinia Bay Area. East. Cape Natur. 67 : 13 - 14.

Olivier, M.C., 1981. An annotated systematic check list of the spermatophyta of the Springs Reserve, Uitenhage. Jl. S. Afr. Bot. 47 : 813 - 828.

- Orians, G.H. & Solbrig, O.T., 1977. A cost-income model of leaves and roots with special reference to arid and semi-arid areas. Amer. Natur. 111 : 677 - 690.
- Paterson, W., 1790. A narrative of four journeys into the country of the Hottentots and Caffraria. London : J. Johnson.
- Paulson, H.A., 1953. A comparison of surface soil properties under mesquite and perennial grass. Ecology 34 : 727 - 732.
- Peet, R.K. & Christensen, N.L., 1980. Succession : a population process. Vegetatio 43 : 131 - 140.
- Penzhorn, B.L. & Olivier, M.R., 1974. A systematic check list of flowering plants of the Addo Elephant National Park. Koedoe 17 : 121 - 136.
- Phillips, J.F.V., 1931. Forest succession and ecology in the Knysna region. Mem. Bot. Surv. S. Afr. 14.
- Phipps, J.P. & Goodier, R., 1962. A preliminary account of the plant ecology of the Chimanimani mountains. J. Ecol. 50 : 391 - 419.
- Pickett, S.T.A., 1976. Succession : an evolutionary interpretation. Amer. Natur. 110 : 107 - 119.
- Pillans, N.S., 1954. A revision of Metalasia. Jl. S. Afr. Bot. 20 : 47 - 90.
- Poore, M.E.D., 1962. The method of successive approximation in descriptive ecology. Adv. Ecol. Res. 1 : 35 - 68.
- Rice, E.L. & Parenti, R.L., 1978. Causes of decreases in productivity in undisturbed tall grass prairie. Amer. J. Bot. 65 : 1091 - 1097
- Roberts, B.R. & Opperman, D.P.J., 1974. Veld management recommendations - a reassessment of key species and proper use of factors. Proc. Grassld. Soc. sth. Afr. 9 : 133 - 140.
- Roberts, B.R., Anderson, E.R. & Fourie, J.H., 1975. Evaluation of natural pastures : quantitative criteria for assessing conditions in the Themeda veld of the Orange Free State. Proc. Grassld. Soc. sth. Afr. 10 : 133 - 140.
- Robson, N.K.B., 1966. Celastraceae. In A.W. Exell, A. Fernandes & H. Wild, eds., Flora Zambeziaca Vol. 2 part 2. London : Flora Zambeziaca Managing Committee.
- Rourke, J.P., 1972. Taxonomic studies on Leucospermum R. Br. Jl. S. Afr. Bot. Suppl. 8.

- Rourke, J.P., 1980. The Proteas of southern Africa. Cape Town : Purnell.
- Rust, I.C., 1967. On the sedimentation of the Table Mountain Group in the western Cape Province. D.Sc. thesis, University of Stellenbosch (unpublished).
- Schulze, B.R., 1972. South Africa. In J.H. Griffiths, ed., World Survey of climatology. Vol. 10. Climates of Africa. Amsterdam : Elsevier.
- Schulze, R.E., 1975. Incoming radiation on sloping terrain : a general model for use in southern Africa. Agrochemophysika 7 : 55 - 61.
- Schulze, R.E. & McGee, O.S., 1978. Climatic indices and classification in relation to the biogeography of southern Africa. In M.J.A. Werger, ed., Biogeography and ecology of southern Africa. The Hague : Junk.
- Schweitzer, F.R. & Scott, K., 1973. Early occurrence of domestic sheep in sub-Saharan Africa. Nature 241 : 547.
- Sclater, J.C., Hellinger, S. & Tapscott, C., 1977. The palaeobathymetry of the Atlantic ocean from the Jurassic to the present. J. Geol. 85 : 509 - 552.
- Scott, J.D. & Van Breda, N.G., 1937. Preliminary studies on the root system of the rhenosterbos (Elytropappus rhinocerotis) on the Worcester Veld Reserve. S. Afr. J. Sci. 33 : 560 - 569.
- Silvester, R., 1960. Stabilization of sedimentary coastlines. Nature 188 : 467 - 469.
- Skead, C.J., 1980. Historical mammal incidence in the Cape Province. Vol. 1. The western and northern Cape. Cape Town : Cape Dept. Nature and Environmental Conservation.
- Slatyer, R.O., ed., 1976. Dynamic changes in terrestrial ecosystems : patterns of change, techniques for study and applications to management. M.A.B. Tech. Notes No. 4 Paris : UNESCO.
- Smit, N.L., 1943. Reclamation of rhenosterbushveld. Farming in South Africa 18 : 287 - 289.
- Smith, H.J., 1967. Ondersoek na die bestuur en benutting van die skynfynbosveldtipe in die Humansdorp grondbewaringdistrik. Department of Agricultural Technical Services, Eastern Cape Region (unpublished).
- Sparrman, A. 1785. Voyage to the Cape of Good Hope. Vol. 2. London.
- Specht, R.L., 1979. Heathland and related shrublands of the world. In R.L. Specht, ed. Heathlands of the world. A. Descriptive studies. Amsterdam : Elsevier.

- Specht, R.L. & Moll, E.J., 1982. Heathlands and sclerophyllous shrublands - an overview. In F.J. Kruger, D.T. Mitchell & J.U.M. Jarvis, eds., Mediterranean-type ecosystems. The role of nutrients. Berlin, Heidelberg, New York : Springer (in press).
- Specht, R.L. Connor, D.J. & Clifford, H.T., 1977. The heath-savanna problem; the effect of fertilizers on sand-heath vegetation of North Stradbroke Island, Queensland. Aust. J. Ecol. 2 : 179 - 186.
- Squires, V.R. & Trollope, W.S.W., 1979. Allelopathy in the karoo shrub, Chrysocoma tenuifolia. S. Afr. J. Sci. 75 : 88 - 89.
- Steedman, A., 1835. Wanderings and adventures in the interior of southern Africa. London : Longmans.
- Stinder, H.W., Cilliers, P.G., Joubert, J.G. & Perold, I.S., 1965. The nutritive value of natural pastures in the Humansdorp area of the south east Cape Province of the Republic of South Africa. Technical Communications 45. Pretoria : Department of Agricultural Technical Services.
- Story, R., 1952. A botanical survey of the Keiskammahoek district. Mem. Bot. Surv. S. Afr. 27.
- Tansley, A.G., 1935. The use and abuse of vegetational concepts and terms. Ecology 16 : 284 - 307.
- Taylor, H.C., 1955. Forest types and floral composition of Grootvadersbosch. Journal of the South African Forestry Association 26 : 33 - 46.
- Taylor, H.C., 1961. Ecological account of a remnant coastal forest near Stanford, Cape Province. Jl. S. Afr. Bot. 23 : 153 - 165.
- Taylor, H.C., 1969. A vegetation survey of the Cape of Good Hope Nature Reserve. M.Sc. Thesis, University of Cape Town (unpublished).
- Taylor, H.C., 1970a. I.B.P. checklist for the Robberg Nature Reserve. Stellenbosch : Botanical Research Institute (unpublished report).
- Taylor, H.C., 1970b. I.B.P. checklist for the Riversdale Nature Reserve. Stellenbosch : Botanical Research Institute (unpublished report).
- Taylor, H.C., 1972. Notes on the vegetation of the Cape Flats. Bothalia 10 : 637 - 646.
- Taylor, H.C., 1978. Capensis. In M.J.A. Werger, ed. Biogeography and ecology of southern Africa. The Hague : Junk.

- Taylor, H.C. & Morris, J.W., 1981. A brief account of coastal vegetation near Port Elizabeth. Bothalia 13 : 519 - 525.
- Taylor, H.C. & Van der Meulen, F., 1981. Structural and floristic classification of Cape Mountain Fynbos on Rooiberg, southern Cape. Bothalia 13 : 557 - 567.
- Thunberg, K.P., 1796. Travels in Europe, Africa and Asia. Vol. 1. Performed between the years 1770 and 1779. London : Richardson, Cornhill and Egerton.
- Tinley, K.L., 1967. The moist evergreen forest - tropical dry semi-deciduous forest tension zone in north-eastern Zululand and hypotheses on past temperate/montane rain forest connections. In E.M. van Zinderen Bakker, ed. Palaeoecology of Africa 2. Cape Town : Balkema.
- Tinley, K.L., 1975. Habitat physiognomy, structure and relationships. In Die Soogdier Navorsingsinstituut 1966 - 1975. Symposium Proceedings. Univ. Pretoria Publ. New Series No. 97 : 67 - 77.
- Tinley, K.L., 1977. Framework of the Gorongosa ecosystem. D. Sc. thesis, University of Pretoria. Published by K.L. Tinley.
- Trapnell, C.G., Friend, M.T., Chamberlain, G.T. & Birch, H.F., 1976. The effect of fire and termites on Zambian woodland soil. J. Ecol. 64 : 577 - 588.
- Trollope, W.S.W., 1970. A consideration of macchia (fynbos) encroachment in South Africa and an investigation into methods of macchia eradication in the Amatole Mountains. M. Sc. thesis, University of Natal, Pietermaritzburg (unpublished).
- Trollope, W.S.W., 1973. Fire as a method of controlling macchia (fynbos) vegetation in the Amatole Mountains of the eastern Cape. Proc. Grassld. Soc. sth. Afr. 8 : 35 - 41.
- Trollope, W.S.W., 1974. Role of fire in preventing bush encroachment in the eastern Cape. Proc. Grassld. Soc. sth. Afr. 9 : 67 - 72.
- Trollope, W.S.W., 1980. Encroachment and control of indigenous undesirable plants in the eastern Cape. Alice : Agricultural Development Research Institute, University of Fort Hare.

- Tyson, P.D., 1964. Berg winds of South Africa. Weather 19 : 7 - 11.
- Van der Merwe, C.V., 1976. Die plantekologiese aspekte en bestuursprobleme van die Goukamma-Natuurreservaat. M.Sc. thesis, University of Stellenbosch (unpublished).
- Van der Merwe, C.V., 1977. 'n Plantegroeiopname van die De Hoop Natuurreservaat. Bontebok 1 : 1 - 29.
- Van der Meulen, F., 1979. Plant sociology of the Western Transvaal Bushveld, South Africa. A syntaxonomic and synecological study. Dissertationes Botanicae. Band 49. Vaduz : J. Cramer.
- Van der Schijff, E. & Schoonraad, E., 1971. The flora of the Mariepskop complex. Bothalia 10 : 461 - 500.
- Van Hulst, R., 1978. On the dynamics of vegetation : patterns of environmental and vegetational change. Vegetatio 38 : 65 - 76.
- Vogel, J.C., Fuls, A. & Ellis, R.P., 1978. The geographical distribution of Kranz grasses in South Africa. S. Afr. J. Sci. 74 : 209 - 215.
- Von Breitenbach, F., 1974. Southern Cape forests and trees. Pretoria : Government Printer.
- Walker, B.R., Ludwig, D., Holling, C.S. & Peterman, R.M., 1981. Stability of semi-arid grazing systems. J. Ecol. 69 : 473 - 498.
- Watson, J.P., 1967. A termite mound in an iron age burial ground in Rhodesia. J. Ecol. 55 : 663 - 669.
- Weather Bureau, 1954. Climate of South Africa. Part 2. Rainfall statistics. Pretoria : Weather Bureau, WB 20.
- Weimarck, H., 1941. Phytogeographical groups, centres and intervals within the Cape flora. Lunds Universitets Arsskrif. N.F. Adv. Z Bd. 37, Nr 5 : 1 - 143.
- Wellington, J.H., 1955. Southern Africa. A geographical study. Vol. 1. Cambridge : Cambridge University Press.
- Werger, M.J.A., 1972. Species area relationships and plot size : with some examples from South African vegetation. Bothalia 10 : 583 - 594.
- Werger, M.J.A., 1974. On concepts and techniques applied in the Zurich-Montpelier method of vegetation survey. Bothalia 11 : 309 - 323.

- Werger, M.J.A., 1978. Biogeographical division of southern Africa. In M.J.A. Werger, ed. Biogeography and ecology of southern Africa. The Hague : Junk.
- Werger, M.J.A., Kruger, F.J. & Taylor, H.C., 1972. A phytosociological study of the Cape fynbos and other vegetation at Jonkershoek, Stellenbosch. Bothalia 10 : 599 - 614.
- Werger, M.J.A. & Van Gils, H., 1978. Phytosociological classification in chorological borderline areas. J. Biogeogr. 3 : 49 - 54.
- Westhoff, V. & Van der Maarel, E., 1973. The Braun-Blanquet approach. In R.H. Whittaker, ed., Ordination and classification of communities. The Hague : Junk.
- Westman, W.E., 1981. Diversity relations and succession in Californian coastal sage scrub. Ecology 62 : 170 - 184.
- White, F., 1971. The taxonomic and ecological basis of chorology. Mitt. Bot. Staatssamml. Munchen. 10 : 91 - 112.
- White, F., 1978. The Afromontane region. In M.J.A. Werger, ed., Biogeography and ecology of southern Africa. The Hague : Junk.
- White, F., 1981. The history of the Afromontane archipelago and the scientific need for its conservation. Afr. J. Ecol. 19 : 33 - 54.
- White, F. ed., 1982. Vegetation of Africa. Paris : UNESCO/AETFAT/UNSO (in press).
- White, A., Dyer, R.A. & Sloane, B.L., 1941. Succulent Euphorbiaieae of southern Africa. Vol. 1 and 2. Pasadena : Abbey Garden Press.
- Whittaker, R.H., 1953. A consideration of climax theory : the climax as population and pattern. Ecol. Monogr. 23 : 41 - 78.
- Whittaker, R.H., 1967. Gradient analysis of vegetation. Biol. Rev. 42 : 207 - 264.
- Whittaker, R.H., 1973. Direct gradient analysis : techniques and results. In R.H. Whittaker, ed. Ordination and classification of communities. The Hague : Junk.
- Whittaker, R.H., Niering, W.A. & Crisp, M.D., 1979. Structure pattern and diversity of a mallee community in New South Wales. Vegetatio 39 : 65 - 76.

Wild, H., 1952. The vegetation of Southern Rhodesia termitaria. Rhodesia agric.
J. 49 : 280 - 292.

Williams, I.J.M, 1972. A revision of the genus Leucadendron. Contrib. Bolus
Herb. 3 : 1 - 425.

PAPER 2

PHYTOCHOROLOGY AND VEGETATION HISTORY IN THE SOUTH EASTERN
CAPE, SOUTH AFRICA.

ABSTRACT

Using the results of a descriptive and an historical approach, hypotheses are presented on vegetation history during a glacial-interglacial sequence in the chorologically complex south eastern Cape. In the descriptive approach 879 taxa from fynbos, renosterveld, subtropical thicket and Afromontane forest communities were classified into phytochorological groups according to their distribution relative to major African phytochoria. The relative occurrence of these phytochorological groups in the different communities was determined and their relationships to environmental variables were explored using correlation and regression analysis. Groups characteristic of Cape shrublands were associated with frequently burnt and grazed conditions and shallow, stony, sandy and infertile soils. Groups characteristic of forest and thicket were associated with unburnt and ungrazed sites and deep, fertile soils. Karroid groups showed strong negative correlations with annual rainfall. Levels of endemism were highest for Cape taxa in fynbos, and succulent karroid taxa in dry thicket. Very few subtropical and Afromontane endemics were recorded. In an historical approach, the palaeoenvironment of the Cape coastal region during the last glacial maximum to Holocene sequence was discussed briefly as a model for predicting vegetation change. Available data on phylogeny, speciation and endemism of taxa characteristic of S.E. Cape phytochoria were discussed in their historical perspective. From a consideration of the descriptive and historical components of the study the following hypotheses on vegetation history were generated. Cape fynbos has had a long history in the S.E. Cape and elsewhere in the Cape Region. Its distribution on edaphic "islands" associated with infertile soils derived from quartzites and sandstones of the mountains would not have been disrupted to any extent, during a glacial-interglacial cycle. Renosterveld is a chorologically complex vegetation type whose distribution on the moderately fertile soils in the Cape Region would have fluctuated dramatically depending on prevailing climatic conditions. Subtropical thicket and grassland and Afromontane forest would have been largely displaced from the Cape Region during the last glacial and would have only become established on certain edaphic sites in the area, with the onset of a warmer, wetter Holocene climate. Karroid taxa have had a lengthy history in the S.E. Cape and during drier glacial times karroid communities would have occupied much of the terrain presently supporting renosterveld and thicket.

CONTENTS

	Page
Introduction	131
Study area	136
Physiography geology and soils	136
Climate	139
Vegetation	142
Methods of data collection and analysis	144
Data collection	144
Species distributions	146
Phytochorological groups	146
Endemics and endem centres	154
Statistical analysis	156
Analysis of phytochorological patterns and endemism	156
Descriptive approach	156
Community chorological patterns and endemism	157
Correlation and regression analysés	167
Historical approach	178
Palaeoenvironments and vegetation change	179
Phylogeny, speciation and endemism	182
Vegetation history in the S.E. Cape : hypotheses	187
Cape Fynbos Shrublands	187
Cape Transitional Small-leaved Shrublands	189
Subtropical Transitional Thicket	192
Afromontane Forest	193
Concluding Remarks	193
References	196

INTRODUCTION

The south eastern (S.E.) Cape, here defined as the area south of the Sneeuwberg–Winterberg–Amatole escarpment and ranging along the coast from about Knysna to the Great Kei River (Fig. 1; see also Gibbs Russel & Robinson, 1981) is a region of immense transition and complexity. It forms a major climatic, topographic and geological transition zone and is consequently a focus of convergence for four phytochoria (Goldblatt, 1978; Werger, 1978a; Werger & Coetzee, 1978; Gibbs Russel & Robinson, 1981; White, 1982).

It is in the S.E. Cape that the east-trending axes of the Cape Folded Belt (Wellington, 1955) sink beneath the sediments of the Karoo Supergroup (Du Toit, 1966). Tertiary planation has greatly subdued the topography of the Folded Belt and it is only west of the Sundays River that there is the rugged mountain topography typical of the southern and south western Cape. The topography of the coastal forelands and interior basins north of the coastal ranges is fairly level, broken only by the wide and often deep valleys of the larger rivers (Kei, Fish, Sundays and Gamtoos) (Fig. 1). Major soil types follow closely the geological substrate so that the S.E. Cape represents the easternmost limit in the Cape of infertile sandy soils derived from the sandstones and quartzites of the Cape Supergroup.

Along the coast the climate ranges from a warm temperate humid to perhumid forest climate in the south west to a subtropical humid to subhumid forest climate in the north east. The moist coastal conditions are interrupted by the warm semi-arid climates of the major river valleys. These valleys become increasingly drier inland and are particularly arid in the interior basins between the coastal mountains and the escarpment (Anon., 1942). The valley climates are very variable with high diurnal and annual temperature ranges and an erratic rainfall (Anon., 1942; Louw, 1976). The coastal mountains of the south west receive much orographic precipitation but because of rainshadow effects, rainfall gradients can be very steep. Rainfall distribution throughout the area is essentially bimodal with spring and autumn peaks. However in the south west, particularly on the coast, the summers are fairly dry whereas in the north east, lowest rainfall is recorded in the winter months (Anon., 1942; Heydorn & Tinley, 1980).

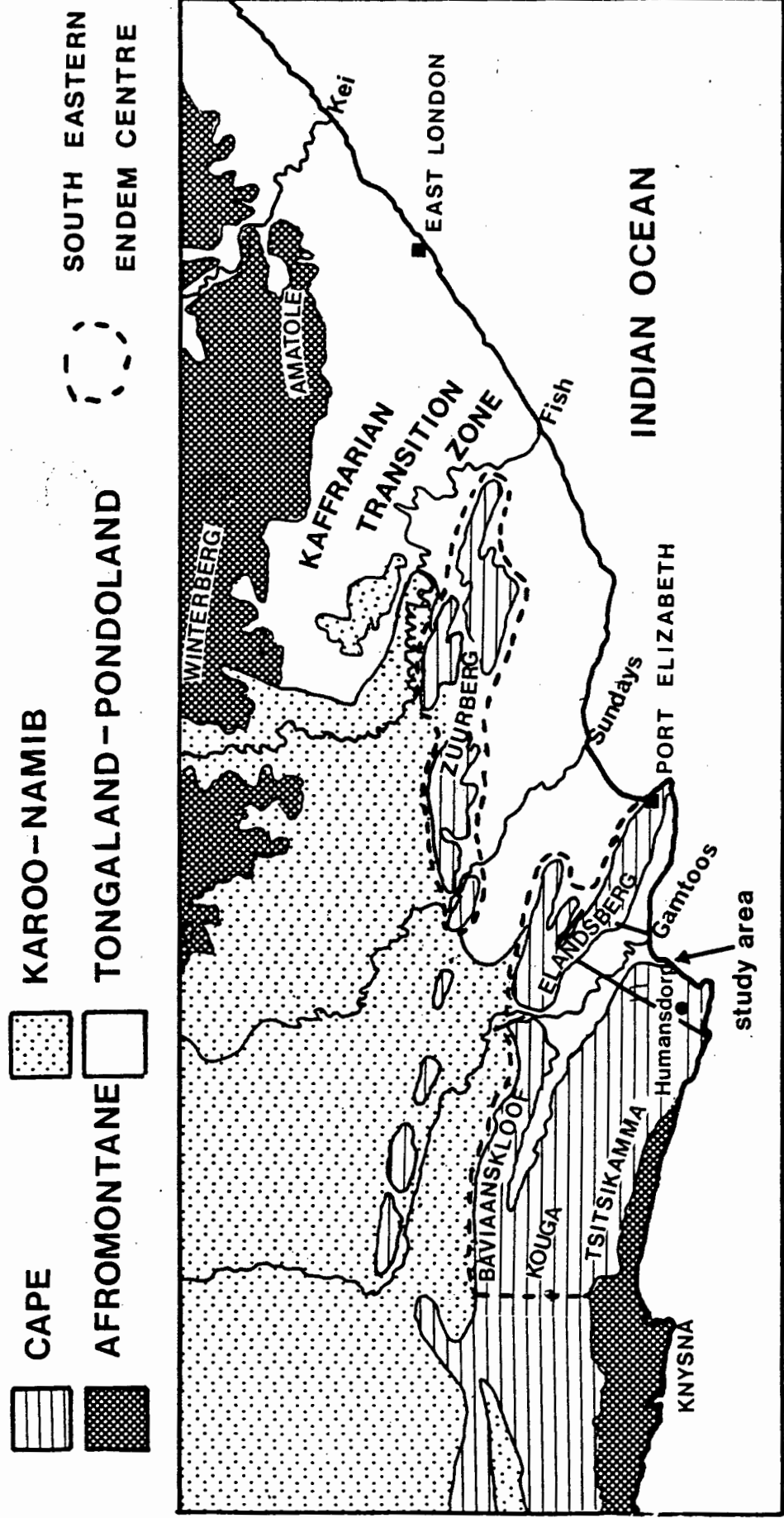


FIG.1. Map of the S.E. Cape showing the approximate boundaries of the phytochorological regions, endem centres and the location of the Humansdorp study area.

The S.E. Cape has long been noted for its phytogeographical complexity. Table 1 shows that S.E. Cape floras (Humansdorp, Albany and Bathurst) have a composition which is clearly transitional between a typical Cape flora and a subtropical flora (Natal) in southern Africa. A further characteristic of the region is that it is where many taxa of diverse phytochorological affinities reach the limits of their distribution, and the proportion of endemics is low relative to rich endem centres in southern Africa (Table 2; see also Gibbs Russel & Robinson, 1981 (Tables 1, 2, 3 and 4)). The S.E. Cape comprises a huge tension zone where four major phytochoria converge (Fig. 1). Tongaland-Pondoland forest and thicket (Moll & White, 1978) enters the region along the coast and penetrate up the river valleys. Succulent and dwarf shrublands of the Karoo-Namib Region (Werger, 1978a) extend down the dry river valleys from the arid interior. Because of increased latitude compensating for altitude, Afromontane (White, 1978) elements are found at sea-level in the S.E. Cape, especially in the south west where the coastal forests are almost entirely composed of Afromontane species. Fynbos taxa of the Cape Region (Taylor, 1978) are strongly represented on the infertile sandy soils derived from Cape Supergroup rocks. The result of this chorological complexity is a mosaic of communities each with different chorological affinities or communities with a chorologically mixed flora. Goldblatt (1978) states: "The eastern Cape, a meeting point of four floristic zones, is especially complex and to define this area (phytochorologically) without extensive research, creates more problems than it solves".

Tension zones between phytochoria provide excellent natural laboratories to study the ecological factors governing the biogeographic delimitation. This information is an important input for the formulation of hypotheses on vegetation history. I have chosen to study intensively a sample flora from the Humansdorp region (Fig. 1), an area which reflects most of the vegetational variation and complexity of the S.E. Cape. The sample flora has been compiled from floristic lists of a number of plots, located in the diverse vegetation types in the study area, and sampled for a phytosociological analysis (Cowling, 1982a).

Biogeographic studies have two main components, a descriptive or static component and an historic or dynamic one (White, 1971; Ball, 1976). In a descriptive approach I established generalized distribution patterns or tracks (cf. Croizat, 1962; Croizat, Nelson & Rosen, 1974) for taxa of the sample flora, determined their relative frequency in the plant

TABLE 1. The number of species contained by the 10 largest families in some southern African floras

Southern Africa ¹	Cape Region ¹	Humansdorp District ²	Albany and Bathurst Districts ³	Natal ⁴
Compositae	2 072	1 034	306	298
Aizoaceae	2 020	765	152	182
Leguminosae	1 495	728	147	151
Liliaceae	907	624	119	142
Iridaceae	840	606	101	102
Ericaceae	799	369	100	100
Gramineae	743	322	93	98
Asclepidaceae	605	315	81	85
Scrophulariaceae	515	250	79	76
Orchidaceae	461	242	64	67
No. spp. in 10 largest families	10 457	5 255	1 239	1 301
Total no. spp in flora	18 532	8 550	2 440	2 389
Area covered (km ² x 10 ³)	2 573	89	5.1	4.8
				87.0

¹ Data from Goldblatt (1978)² Data from Fourcade (1941)³ Data from Martin & Noel (1960)⁴ Data from Ross (1973)

TABLE 2. Distribution of taxa in the S.E. Cape

	\longrightarrow 1	Distribution (% total taxa) \longleftarrow 2	\longleftrightarrow 3	Endemic 4
This study n = 879	43.1	8.8	32.1	14.6
Trees in Coates Palgrave (1977) n = 319	10.6	49.5	36.0	3.8

1 Taxa from the S and W whose distributions terminate in the S.E. Cape

2 Taxa from the N and E " " " " "

3 Taxa whose distributions extend through the S.E. Cape

4 Taxa endemic to the S.E. Cape (S.E. Centre or Kaffrarian Transition Zone)

communities and correlated this frequency with ecological site factors. I formulated inductively based narrative hypotheses (cf. Ball, 1976) to explain these relationships in the study area. In an historical approach I reviewed evidence on paleoenvironments and examined phylogenetic histories, speciation patterns and endemism of taxa representative of the different tracks in order to give a causal historical explanation of these distribution patterns. Assuming that the ecological factors determining the present day distributions of biogeographic elements have not differed drastically during, at least, the last glacial maximum to Holocene sequence, I propose generalized hypotheses to explain vegetation history during this period in the S.E. Cape. These hypotheses can be generalized for the entire Cape Region and adjacent phytochoria, and yield predictions that can be tested using independent lines of evidence.

STUDY AREA

The study area is in the Humansdorp region of the S.E. Cape (Fig. 1). Vegetation types typical of the Cape, Tongaland-Pondoland and Afromontane phytochoria are well represented while karroid elements are conspicuous in the dry valleys. The region qualifies in all respects as a study site to investigate biogeographical complexity of the S.E. Cape. I present below a brief sketch of the environment and vegetation of the area. More details are given in Cowling (1982a).

Physiography, geology and soils

Both physiographic elements of the Cape coastal region are present in the Humansdorp area. The rugged quartzitic sandstone mountains of the Cape Folded Belt (Wellington, 1955) are represented by the Elandsberg mountains (700 – 1 000 m) north of the Gamtoos valley (Fig. 1) and some low remnant anticlines (300 – 400 m) north of Humansdorp. The Coastal Forelands (Wellington, 1955) comprise a low (0 – 300 m) Tertiary plain of subaerial and marine abrasion (King, 1972). A third feature is the wide alluvial valley and braided course of the Gamtoos River. This river, which breaches the Folded Belt in a striking fashion, has its origins in the mountains of the Great Karoo.

The oldest rocks in the region belong to the late Precambrian Congo Formation of the Malmesbury Supergroup. They occur in a faulted block truncating the southern limb of the Elandsberg range. The beds consist largely of phyllites with two thick horizons of limestone (Haughton, Frommurze & Visser, 1937).

Rocks of the Cape Supergroup predominate in the area. Quartzitic sandstones of the Table Mountain Group (T.M.G.) comprise the mountains but also underlie considerable portions of the coastal plain. Argillaceous Bokkeveld beds occur extensively on the coastal plain.

Cretaceous fluvial, estuarine and marine sediments of the Uitenhage Group are found in the Gamtoos valley. Coarse grained conglomerates and sandstones are the predominant rocks. The lower beds are finer and consist of fine sandstones with reddish marls and grey sandy clays.

Quaternary deposits occur as alluvium in the major river valleys and as calcareous dune sands along the coast, where there are occasional exposures of calcrete.

Soils are highly variable. Fertility status, and to a lesser degree, structure, are correlated with parent material. I recognize four soil categories on the basis of topsoil (0 - 25 cm) fertility, which plays a major role in the delimitation of plant communities (Cowling, 1982a). "Fertility" is defined relative to the requirements of common crop and pasture plants. Soil data are shown in Table 3.

(i) Infertile sands.

Soils are strongly acid loamy sands to sandy loams derived from Table Mountain Group quartzites and Cretaceous sandstones and conglomerates. They have low levels of all major nutrients and support fynbos vegetation (Table 3). Soil depth and drainage varies considerably: a typical catena shows a gradation from shallow rocky leached soils on steep mountain slopes to deeper, sometimes poorly-drained types on pediments and in valley fills. The infertile sands correspond to Specht & Moll's (1982) "nutrient-poor" suite.

(ii) Fertile loams.

These soils are usually deep (> 1m) weakly acid loams, sandy loams or sandy clay loams. With the exception of the dune sands (see below) they occur on all parent materials and invariably support thicket vegetation (Table 3). On T.M.G. quartzites they are largely restricted to colluvial sites. These soils have generally high levels of organic carbon which has a favourable effect on phosphorus, nitrogen and cation exchange capacity (Brady, 1974). Water holding capacity is also improved. The maintenance of high levels of organic matter is probably plant induced (cf. Aweto, 1981). Fertile loams are also associated with

TABLE 3. Syntaxonomic hierarchy and some environmental relationships for communities in the study area

Syntaxa	Geology	Rainfall (mm yr ⁻¹)	Altitude (m)	pH	Sand (%)	Silt (%)	Clay (%)	S-value (meq. %)	Exchange- able Ca (ppm)	Oxidiz- able Carbon (%)	Total Nitro- gen (%)	Available Phospho- rus (ppm)	No. of soil samples
CLASS: CAPE FYNBOS SHRUBLANDS Order : South Eastern Mountain Fynbos <u>Tetradlea capillacea</u> - <u>Thomomus multiflorus</u> community <u>Leucospermum cuneiforme</u> - <u>Tetradlea thermalis</u>	T.M.G. quartzite T.M.G. quartzite/ Cretaceous sandstone	800-1000 700-300	400-700 300-400	4.1± 4.0	18.9± 78.0	2.7 13.8	4.8± 8.2	2.2 3.3	273± 371	3.8± 3.3	0.8± .07	2.5± 3.0	4 1
Order: Grassy Fynbos <u>Thamnochortus glaber</u> - <u>Erica diaphana</u> <u>Protea neriifolia</u> - <u>Clusia alaternoides</u> <u>Erica pectinifolia</u> - <u>Trachypogon spicatus</u>	T.M.G. quartzite T.M.G. quartzite T.M.G. quartzite/ Cretaceous sandstone	650-700 650-700 550-650	80-100 200-400 120-300	4.3± 4.5± 4.7±	19.8± 179.7± 284.7±	.3 .4 7.9	.5± .9± 4.5±	.2 .3 1.7	187± 630± 430±	2.9± 5.9± 3.9±	.3 1.6± 1.4±	1.4± 5.8± 3.2±	3 4 9
<u>Themeda triandra</u> - <u>Passerina pendula</u>	Cretaceous con- glomerate	450-500	60-100	4.3	89.2	6.0	4.6	3.7	440	2.5	.08	2.8	2
<u>Thamnochortus fruticosus</u> - <u>Tristachya leucothrix</u>	T.M.G. quartzite	650-700	90-330	4.7±	39.8±	.3	.6±	.2	320±	2.8±	0.8±	2.6±	5
Order : South Coast Dune Fynbos <u>Restio eleocharis</u> - <u>Agathosma stenopetala</u> <u>Restio eleocharis</u> - <u>Maytenus procumbens</u> <u>Themeda triandra</u> - <u>Stenotaphrum secundatum</u>	Recent sand & calccrete Recent sand Recent sand	650-850 600-700 600-800	0-80 0-60 0-60	7.0± 7.5± 7.4±	2.96± 299.3± 699.2±	5.1 .3 .5	.3± .4± .4±	.3 .2 .2	14.9± 14.4± 12.0±	6.2± 7.3± 3.5±	1.3 1.8 2.0	5.4 18.3 13.1	3 5 6
CLASS: CAPE TRANSITIONAL SMALL-LEAVED SHRUBLANDS Order : South Coast Renosterveld <u>Themeda triandra</u> - <u>Cliffortia linearifolia</u> <u>Elytropappus rhinocerotis</u> - <u>Eustachys sparganoides</u>	Bokkeveld shale Cretaceous con- glomerate	650-700 450-500	30-85 60-90	5.1± 4.7±	15.9± 386.1±	10.4± 11.6±	16.2± 2.6±	13.9 4.2	6.3± 6.3±	4.0± 6.8±	1.0 1.1	3.8± 7.5±	8 5
<u>Elytropappus rhinocerotis</u> - <u>Metastasis muricata</u> <u>Elytropappus rhinocerotis</u> - <u>Relbunium genistaeifolia</u>	Bokkeveld shale Bokkeveld shale	500-550 450	50-200 170-230	5.5± 5.4	46.1± 61.6	3.9± 19.1	18.1± 19.8	7.4 7.8	869± 754	4.9± 7.8	1.4 2.3	3.2± 3.9	8 1
CLASS: AFROMONTANE FOREST Order : Kynsna Afromontane Forest <u>Rapanea melanophloea</u> - <u>Ocotea bullata</u> <u>Rapanea melanophloea</u> - <u>Ceanothus inermis</u>	T.M.G. quartzite T.M.G. quartzite/ Congo phyllite	900-1000 750-850	500-550 350-500	3.4 4.1	65.9 69.5	21.1 23.5	13.1 7.5	6.3 6.6	566 635	12.7 9.3	.51 .30	11 18	2 2
CLASS: SUBTROPICAL TRANSITIONAL THICKET Order : Kaffrarian Thicket <u>Pterocelastrus tricuspidatus</u> - <u>Gonioma kamassi</u> <u>Pterocelastrus tricuspidatus</u> - <u>Euclea undulata</u>	T.M.G. quartzite Bokkeveld shale/Congo phyllite & limestone	550-700 500-650	10-160 10-300	5.4± 5.9±	8.74± 5.60±	9.8± 2.2±	10.7± 16.5±	11.1 8.7	19.6± 21.7±	12.5± 12.4±	4.4 5.8	2.6 9.7	4 9
<u>Cassine aethiopica</u> - <u>Cussonia thyrsiflora</u> <u>Cassine aethiopica</u> - <u>Schotia afra</u>	Recent sand Recent sand	600-800 500	10-55 15-40	7.4± 7.2	9.99± 99.0	.2 .4	.3± .6	.1 .4	16.0± 18.4	6.7± 6.5	3.6 2.6	5.0 10.7	5 1
Order: Kaffrarian Succulent Thicket <u>Sideroxylon inermis</u> - <u>Euphorbia grandiflora</u> <u>Euclea undulata</u> - <u>Brachylaena ilicifolia</u>	Cretaceous shales/ alluvium Bokkeveld shale	450-500 450	5-200 50-150	5.9± 4.8±	1.06± 8.55±	7.8± 13.5±	15.1± 22.9±	4.1 8.2	14.7± 12.6±	4.6± 7.2±	2.2 .8	37.0 9.9	7 300

termitaria thickets where there is little doubt that termite consumption of litter results in high organic matter and a concentration of exchangeable bases (Lee & Wood, 1971). Where annual precipitation exceeds 700 mm soils are strongly acid, low in exchangeable cations, and support forest vegetation (Table 3). Most thicket soils correspond to Specht & Moll's (1982) base-rich suite.

(iii) Loams of intermediate fertility.

These are shallow moderately acid to acid, loam and sandy loam soils derived from Bokkeveld shales and Cretaceous conglomerates. On the shales the soils have a duplex structure and where the terrain is level, they are seasonally waterlogged. Conglomerate soils are stony and well-drained. Fertility status is intermediate between categories (i) and (ii) above. These differences in fertility have a profound effect on the distribution of plant communities (Cowling, 1982a). Loams of intermediate fertility support renosterveld communities (Table 3).

(iv) Calcareous dune sands

The coastal dunes have neutral to alkaline calcium-rich sandy soils. They have high levels of total nitrogen, exchangeable bases and available phosphorus. In calcium-rich alkaline soils phosphates are precipitated in an unavailable form by calcium compounds (Brady, 1974) and, under these conditions, the detection of realistic values of available phosphorus remains problematic. Dune sands support thicket on deep well drained soils and fynbos on shallow soils overlying calcrete and seasonally waterlogged sites in dune hollows (cf. Table 3). Calcareous dune sands correspond to Specht & Moll's (1982) "calcium-rich" soil suite.

Climate

The Humansdorp area falls within the southern warm temperate region (Schulze & McGee, 1978). The climatic régime is dominated by an alternating succession of east-moving cyclones, budded off from the circum-polar westerlies, and high pressure anti-cyclones which ridge in behind the lows (Jackson & Tyson, 1971). In winter the frequency and intensity of cyclonic fronts is greatest, due to a northward migration of the pressure belts. The weather is cool and often rainy. In summer, a strengthening and southward migration of the Atlantic high pressure cell effectively blocks cyclones reaching the south western Cape resulting in a markedly reduced precipitation and the recognition of a mediterranean-type climate (Schulze, 1972). This effect is not felt so strongly along the southern and S.E. Cape coasts which receive a considerable amount of summer rainfall.

Much precipitation on the south and S.E. Cape coasts occurs with the eastward passage of cyclonic low pressure systems which have their highest frequency in winter. However the heaviest downpours are associated with post frontal conditions and "cut-off lows" when cool moist air from the south is advected over the warm Indian Ocean, towards low pressure cells inland (Anon., 1942; Heydorn & Tinley, 1980). Strong southerly post-frontal winds, accompanied by heavy rains are most frequent in autumn and spring, whereas frontal rains, associated with westerly winds, are most common in winter. This rainfall pattern must be clearly distinguished from the pattern in the mediterranean climate region of the south western Cape where most rain is associated with pre-frontal NW winds (Heydorn & Tinley, 1980).

I recognized three climatic types at the mesoclimatic level in the study area. These are a sub-humid coastal plain climate, a semi-arid valley climate and a humid coastal mountain climate. Figure 2 shows climate diagrams for each climatic type.

(i) Coastal plain subhumid climate

The climate is mild with low diurnal and annual temperature ranges. The climatic régime is mediterranean: the summer months (Dec., Jan., Feb.) are hottest and driest. Rain falls with both frontal and post-frontal events.

(ii) Semi-arid valley climate

The river valleys of the S.E. Cape have a warmer, drier and more variable climate than the adjacent mountains and interfluves: temperature extremes are great and rainfall variability is high (Anon., 1942; Louw, 1976). The rainfall in the Gamtoos valley shows a bimodal distribution - heaviest precipitation is associated with post-frontal events whereas most frontal rains miss the valley region.

(iii) Humid coastal mountain climate

In the S.E. Cape where rainfall is under strong orographic control, the highest precipitation is recorded on the coastal axis of the Cape Folded Belt. In the study area the upper seaward slopes of the Elandsberg range receive more than $1\,000\text{ mm yr}^{-1}$ of largely orographic rain, associated with frontal and post-frontal conditions. Rainfall peaks are in autumn and spring. Temperatures are equable but lower than the surrounding lowlands and light frosts and occasional snow are recorded in winter.

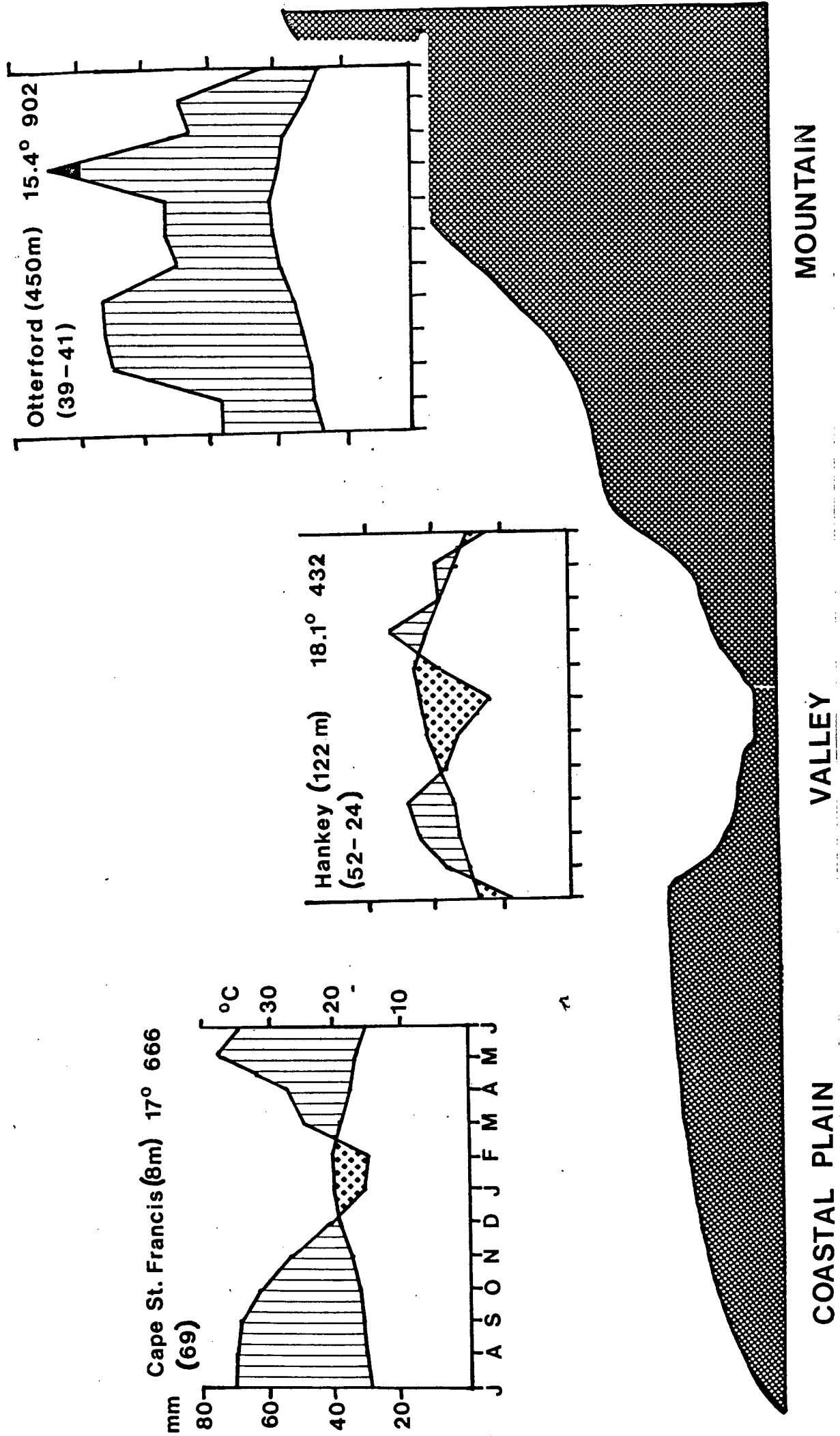


FIG. 2. Climate diagrams representative of the coastal plain, valley and mountain climatic types in the study area. Data from Anon., (1942) and Weather Bureau (1954).

Vegetation

The vegetation of the study area has been classified hierarchically into a series of classes, orders and communities (Cowling, 1982a; see Table 3 for syntaxonomic hierarchy and nomenclature). I explain my class and order concepts briefly below.

(i) Cape Fynbos Shrublands

This class comprises the fynbos shrublands and heathlands of the Cape Floristic Region (for reviews see Taylor, 1978 and Kruger, 1979). They predominate on the acid sandy infertile substrates of the Cape Folded Belt and coastal plain. A distinct group of communities occurs on calcareous alkaline substrates along the southern Cape coast. Cape Fynbos Shrublands have the structural characteristics of the heathland syndrome (small leaves, long-lived leaves, sclerophylly, ever-green hemicryptophytes) (Specht, 1979). Good differential families include the Ericaceae, Restionaceae and Proteaceae (cf. Table 1). In the study area, and generally in the S.E. Cape, there are 3 orders of Cape Fynbos Shrublands.

South Eastern Mountain Fynbos

This order comprises a related group of chorologically pure fynbos communities confined to the upper, moist and poleward slopes of the Cape Folded Belt in the S.E. Cape. Substrates are extremely acid and infertile (Table 3). I recognized two communities in the study area (Table 3).

Grassy Fynbos

Grassy Fynbos communities occur on the north and lower slopes, and planed surfaces of the Cape Folded Belt in the S.E. Cape. They occupy drier, warmer and more fertile sites than the S.E. Mountain Fynbos (Table 3). Grassy Fynbos has a high cover and diversity of subtropical C4 grasses (Themeda, Heteropogon, Trachypogon, Eragrostis, Brachiaria) which largely replace Restionaceae.

I recognized five communities in the study area (Table 3).

South Coast Dune Fynbos

This fynbos type is restricted to calcareous dune sands along the southern and S.E. Cape coasts. It differs from other fynbos types in lacking Proteaceae and having a strong subtropical thicket shrub component (e.g. Rhus, Olea, Maytenus, Rhoicissus, Sideroxylon). I recognized three communities in the study area.

(ii) Cape Transitional Small-leaved Shrublands

This class comprises the non-fynbos small-leaved shrublands of the Cape Region. These shrublands lack the diagnostic fynbos floristic and structural features and are generally restricted to the more fertile soils of the coastal forelands and inter-montane valleys (Table 3). Many of the species are restricted to the Cape Region, but many others are wide ranging generalists. Grasses play a major role in the overall composition and some of these shrublands have been derived from grasslands in historical times (Cowling, 1982a). Cape Transitional Small-leaved Shrublands are represented by a single order in the study area.

South Coast Renosterveld

This shrubland type is restricted to the coastal forelands from near Cape Town to the Grahamstown region of the S.E. Cape. The dominant shrub is Elytropappus rhinocerotis while conspicuous codominants are species of Relhania, Helichrysum, Euryops and Aspalathus. Subtropical grasses, particularly Themeda triandra and numerous geophytes (Oxalis, Ornithogalum, Babiana, Romulea) make up the field layer. I described four South Coast Renosterveld communities from the Humansdorp study area (Table 3).

(iii) Subtropical Transitional Thicket

Subtropical thicket communities penetrate the temperate Cape region as far as the south western Cape where they have been termed "mediterranean shrublands" by Boucher & Moll (1980) and Specht & Moll (1982). Structurally they are best described as a tangle of evergreen, spiny, sclerophyllous shrubs and vines and, in drier regions, have a high cover of succulents. Typical genera are Euclea, Diospyros, Sideroxylon, Rhus, Maytenus, Cassine, Olea, Crassula, Aloe and Euphorbia. In the Cape, thicket is largely confined to well-drained fertile soils of the coastal forelands. These communities have their maximum diversity in the Kaffrarian Transition Zone (Fig. 1; see below) which is centred between the Kei and Gamtoos rivers. There are two orders in the study area and elsewhere in the S.E. Cape.

Kaffrarian Thicket

Kaffrarian Thicket is a non-succulent type which occurs on fairly mesic sites and has strong affinities with Afromontane forests. I described four communities from the study area (Table 3).

Kaffrarian Succulent Thicket.

This thicket type is confined to the hot dry river valleys of the southern and S.E. Cape. It is characterized by a strong incidence of succulents (Euphorbia, Crassula, Aloe, Delosperma) including many species of Karoo-Namib affinity. I recognized two communities in the Humansdorp region (Table 3).

(iv) Afromontane Forest

Afromontane Forests are the temperate African mountain forests distributed in an archipelago of mountain "islands" from Somalia to the Cape Peninsula (White, 1978). In the study area Afromontane forests are restricted to the Elandsberg mountains on colluvial sites with deep soils. I recognized two communities (Table 3) which I placed in the order "Knysna Afromontane Forest" because of their resemblance to the extensive forests of that region.

METHODS OF DATA COLLECTION AND ANALYSIS

The fundamental datum of biogeography is the distribution of a taxon. White (1971) argues that it is more meaningful to analyze the distribution of dominant species rather than attempt a composite analysis of a whole flora. He has characterized phytochoria largely on the basis of the distributions of woody species only (White, 1976a; 1978; 1982). However I feel that for the purpose of chorological analysis it is essential to analyze the distributions of many species of diverse taxonomic groups.

Data collection

I sampled a total of 194 plots (100 m^2) selectively located in the study area (see Cowling, 1982a for details on sampling strategy and Fig. 4 for distribution of samples in the vegetation types). From this sample I compiled a list of 879 taxa (including sub-species but not varieties) whose distributions were determined from herbarium records in the Albany Museum Herbarium, Grahamstown (GRA) and the Bolus Herbarium at the University of Cape Town (BOL). These data were supplemented by studying distribution maps in monographs of recently revised taxa. Voucher specimens of taxa used in this analysis are housed in the Albany Museum Herbarium.

In each sample plot I recorded a range of environmental variables. Table 4 shows these variables with some information on classes and methods. The variables measured include both primary or abiotic factors such as average annual rainfall, aspect, slope and

TABLE 4. Environmental variables recorded in plots. Soil chemical data, from the A horizon only, for a subset of 97 samples. Some details on classes of variables and methods are shown. Abbreviations are those used in Tables 7 - 12, and in the text

Variable	Abbreviation	Classes of variables and methods
VEGETATION AGE (yr)	VAG	Post-fire, post-bush-cut. Estimates based on information from landowners
GRAZING INTENSITY	GRZ	Classes: ungrazed = 1, light = 2, moderate = 3, heavy = 4, over-grazed = 5. Scale based on current stocking rate, past grazing and the effects of grazing (cf. Roberts <i>et al.</i> , 1975)
ANNUAL RAINFALL (mm)	RAI	Data from 1 : 250 000 isohyet maps and local weather stations
ALTITUDE (m)	ALT	From 1 : 50 000 topographic sheets
ASPECT	ASP	Classes: 1 = SE, 2 = S, 3 = SW, 4 = E, 5 = W, 6 = NE, 7 = N, 8 = NW: a cool to hot gradient estimated from aspect-radiation flux data (Schulze, 1975)
SLOPE INCLINATION	SLO	Slope angle in degrees
LITTER COVER (%)	LIT	Subjective estimate
ROCK COVER (%)	RCO	Subjective estimate
SOIL DEPTH (m)	SDE	
% SAND CONTENT	SAN	Estimated for all plots and tested using results of a textural analysis (pipette method) of samples from 97 plots
SOIL pH	PHH	1 N KCl 1 : 2.5 soln.
EXCHANGEABLE CALCIUM (ppm)	CAC) 1 N NH ₄ acetate leachate
S-VALUE (sum of exchangeable cations) (meq %)	BAS	
OXIDIZABLE CARBON (%)	CAR	Walkley-Black method
TOTAL NITROGEN (%)	NIT	Kjeldahl
AVAILABLE PHOSPHORUS (ppm)	PHO	Bray No. 2 (acid extraction, pH 3) Modified Olsen (alkali extraction, pH 8)

measures of soil fertility, as well as biotic factors such as post-disturbance vegetation age and grazing intensity. In the S.E. Cape the disturbance régime can have a profound effect on the composition and phytochorological affinities of vegetation through the invasion and thickening up of certain weedy species (Trollope, 1970; Gibbs Russel & Robinson, 1981). Soil fertility data are available for only 97 of the 194 samples (Table 3).

Species distributions

a. Phytochorological groups

In my analysis of the distribution of taxa in the sample flora I established a number of phytochorological groups which are essentially recurring geographic distributions. These distributions are empirical facts comparable to Croizat's (1962) generalized track. Although there is no a priori reason not to invoke random processes in dispersal and distribution patterns (Vuilleumier & Simberloff, 1980), the establishment of generalized distribution tracks, when combined with a phylogenetic component, usually leads to well formulated and testable hypotheses (Ball, 1976). My phytochorological groups are defined relative to the distribution of taxa in the major African phytochoria. I have used the phytochoria delimited in Werger (1978b) with modifications to the Tongaland-Pondoland and Afromontane Regions according to White (1976a; 1982).

Werger (1978b) presents a detailed account of biogeographical division in southern Africa. There is still some dispute regarding the precise boundaries of the phytochoria, particularly in the S.E. Cape (Goldblatt, 1978; Werger, 1978a; Werger & Coetzee, 1978; See Fig.1). I follow White (1976a; 1982) in not ranking the phytochoria in a hierarchical manner.

The assignation of taxa to phytochorological groups requires a knowledge of both the distribution and ecology of those taxa (White, 1971). Thus two species which transgress a phytochorological boundary and have similar distributions, can be placed in different groups. This happens when one of the species is an "ecological and chorological transgressor species" (White, 1978) occurring in roughly equal abundance in both phytochoria and in vegetation types characteristic of both phytochoria, whereas the other species transgresses the boundary in isolated populations in vegetation typical of the phytochorion where its distribution is centred. These complex distribution patterns are fairly typical of Cape-Afromontane and Cape-Tongaland-Pondoland linking elements. I have made many subjective decisions in allocating species to phytochorological groups. In the section below I discuss the delimitations of the phytochoria, make explicit my assumptions in

defining groups and assigning species to them, and give a range of examples. Maps of species distributions characteristic of the groups are shown in Fig. 3. The abbreviations I use below are those used in Tables 7 - 12.

(i) Cape endemics (CEN)

Since the time of Bolus (1905) students of plant geography in southern Africa have held the view that the flora of the sub-continent could be divided into two main types: a Cape flora confined to the southern and south western Cape, and an African flora occurring in the rest of the area. Today the Cape flora is regarded as one of the world's floral kingdoms (Capensis) while the rest of Africa forms part of the Palearctic Kingdom (Takhtajan, 1969; Good, 1974).

The ecology and biogeography of the Cape Region have been reviewed recently (Goldblatt, 1978; Taylor, 1978; 1980; Kruger, 1979). The area (sensu Goldblatt, 1978) has a very rich flora of approximately 8 550 species and a level of endemism more typical of an island flora than a continental one (Goldblatt, 1978). In this analysis I used Werger's (1978b) delimitation of the region (Fig. 3).

I classified 38.9% of the sample flora from the study area as CEN taxa. They include species of typical Cape genera such as Restio, Hypodiscus, Aspalathus, Erica, Leucadendron, Protea, Phyllis, Passerina and many others. Some CEN species belong to genera which are centred outside the Cape Region, e.g. Crassula ciliata, Euclea polyandra and Rhus rosmarinifolia.

(ii) Afromontane endemics (AEN)

White (1976a; 1978; 1982) drew attention to the distinctness of an Afromontane flora. He recognized the Afromontane region as occupying an archipelago of mountain "islands" from Somalia to the Cape Peninsula with outliers in West Africa (see Fig. 1 in White, 1978). White (1978) defined the region entirely in terms of the distribution of woody taxa largely from the forest flora. However evidence corroborating his delimitation of the region has come from the biogeographical analysis of some herbaceous taxa (e.g. Weimarck, 1941; Clayton, 1976; Linder, 1982). Today much of the Afromontane Region consists of grasslands, secondary or otherwise, with an interspersed of "fynbos" elements. I included the grasslands of the Natal and Transkei midlands and uplands in the Afromontane Region (Fig. 3; White, 1976a; 1982; Linder, 1982).

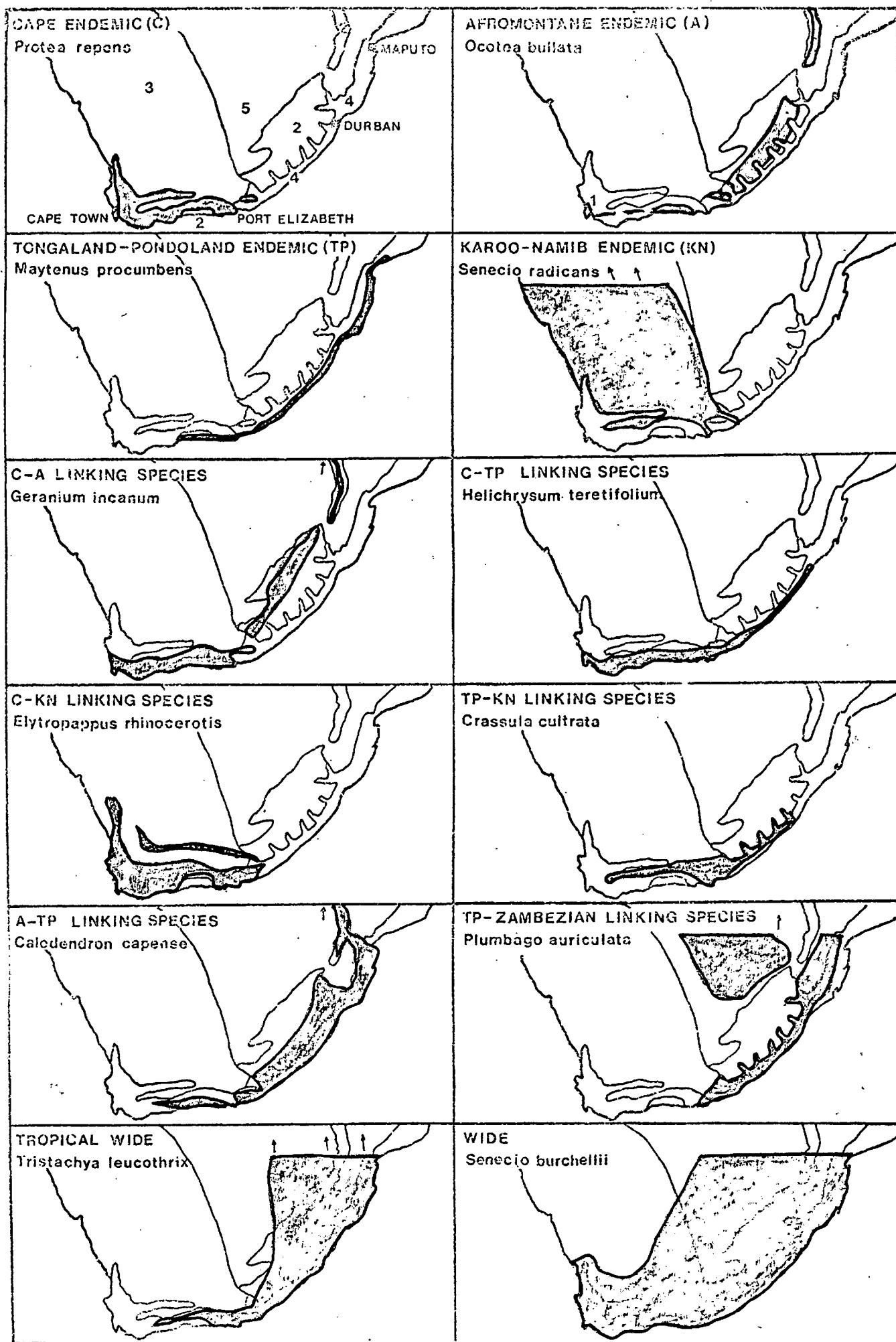


FIG. 3. Distributions of species typical of phytochorological groups. 1=Cape Region; 2=Afromontane; 3=Karoo-Namib; 4=Tongaland-Pondoland; 5=Zambezian.

I classified 9.6% of the sample flora as AEN taxa. The majority of the species are forest trees such as Podocarpus spp., Rapanea melanophloeos, Ocotea bullata, Kiggelaria africana, Nuxia floribunda and Olea capensis ssp. macrocarpa. A smaller component consists of grasses and forbs which occur on the Drakensberg and other Afromontane centres to the north but do not penetrate into the Cape Region beyond the Knysna area. Some examples are Festuca caprina, F. costata, Helictotrichon hirtulum, Sporobolus pectinatus, Gladiolus longicollis, Dierama pendulum, Indigofera heydantha and Bulbostylis humilis. Another group includes herbs of the forest floor (Asplenium splendens, A. erectum, Dryopteris inaequalis, Cheilanthes bergiana and Cyperus albostratus).

(iii) Tongaland-Pondoland endemics (TEN)

White (1976a; 1982) has developed a non-hierarchical chorological analysis of Africa which emphasizes endemism and uses four major categories of equal rank. He treats the Indian Ocean Coastal Belt (Moll & White, 1978) as comprising two Regional Transition Zones and Mosaics of equal rank. The Zanzibar-Inhambane Regional Mosaic occupies a narrow coastal strip from Somalia to the mouth of the Limpopo River while the Tongaland-Pondoland Regional Mosaic extends southwards to Port Elizabeth (Moll & White, 1978).

Along the southern Natal, Transkei and S.E. Cape coasts the Tongaland-Pondoland Region occupies a narrow strip—in some places, where the mountains rise steeply from the coast, less than 8 km wide. It includes the broad coastal plain of northern Natal and penetrates into the interior along the major east coast river valleys (Fig. 3; see Fig. 2 in Moll & White, 1978). The natural vegetation of much of the area is subtropical forest and thicket although this has been much replaced by secondary grassland and thorn thicket (Moll & White, 1978).

I classified 5.1% of the sample flora as TEN species. Most taxa are forest and thicket elements including Erythrina caffra, Maytenus procumbens, Cassine reticulata, Dovyalis rotundifolia, Brachylaena ilicifolia, Euphorbia triangularis, Aloe pluridens, Senecio macroglossus and Cynanchum natalitum. I included Sideroxylon inerme as a TEN species although its distribution spans the entire east African coastal belt from Kenya to the Cape Peninsula. However, west of Knysna it is associated with patches of mature thicket which I regard as penetrations of Tongaland-Pondoland communities into the Cape Region.

(iv) Karoo-Namib endemics (KEN)

The Karoo-Namib region occupies much of the arid and semi-arid south western and western portion of southern Africa (Fig. 3; Werger, 1978a). It has a rich flora with many endemic genera and species (Compton, 1929; Goldblatt, 1978). The south western and southern parts are very rich in succulents (Aizoiaceae-Mesembryanthemoideae, Euphorbiaceae, Asclepiadaceae, Crassulaceae, Geraniaceae, Liliaceae, Compositae). Many genera have radiated extensively in the karroid succulent veld of these regions.

In the S.E. Cape, Karoo-Namib taxa penetrate to the coast along the hot dry valleys of the Fish, Sundays and Gamtoos rivers. I classified 4.0% of the Humansdorp sample flora as KEN species. These include many succulents (Crassula capitella ssp. thyrsiflora, C. muscosa, Senecio radicans, S. articulata, Delosperma echinatum, Psilocaulon pubescens, Pachypodium bispinosum) and fewer non-succulent dwarf shrubs (Sutera pinnatifida, Hermannia filifolia, Asparagus striatus, Helichrysum zeyheri, Blepharis capensis).

(v) Cape-Afromontane linking species (CAL)

Isolated patches of fynbos comprising species of genera usually regarded as "typical" Cape elements (Protea, Erica, Muraltia, Passerina, Restio) extend along the east African mountains from the eastern Cape Drakensberg to the Ethiopian highlands (see Killick, 1979 for a review of Afromontane fynbos communities). Most phyto-chorological maps delineate the boundary between the Cape and Afromontane regions as corresponding with the low hot valleys of the Fish River and its tributaries (Fig. 1; White, 1976a; 1982; Werger, 1978b). This latter region is the Kaffrarian Interval of Weimarck (1941). The Afromontane enclaves west of this line are characterized on the basis of forest floras only (White, 1978). That the distinction between the Cape and Afromontane regions is fully justified is still a matter of dispute (Tinley, 1975; Linder, 1982).

Weimarck (1941) drew attention to a Cape-Afromontane flora which demonstrates strong links between the Cape and Afromontane regions (see also Wild, 1968). Afromontane species belonging to Cape-centred genera are often the least specialized members of the genus (Levyns, 1938; 1952; 1954; 1958; 1964; Beard, 1959; Wild, 1968; Rouike, 1972). Some workers (Levyns, 1964; Wild, 1968) state that there existed an uninterrupted Cape-Afromontane flora when there

was a continuous elevated belt along the east African escarpment in the Tertiary (King, 1978). Subsequent peneplanation is invoked to explain the enormous present day disjunctions shown by many of the species in the Afromontane region (Croizat, 1962; Levyns, 1964; Wild, 1968). Whether these genera have migrated southwards into the Cape Region where they have undergone "massive speciation" (Levyns, 1964) or have migrated northwards from the Cape (Williams, 1972; Linder, 1982) is a matter to be considered for each genus separately (cf. Axelrod & Raven, 1978).

Killick (1963) presents evidence showing that the flora of the Natal Drakensberg is more allied to the flora of the Cape Region than that of the Chimanimani mountains of Zimbabwe. In her phytogeographical analysis of the compositae of Natal, Hilliard (1978) has shown that the high mountain flora of Natal is largely autochthonous and links to the Afromontane Region of tropical Africa are extremely tenuous. However, at the species level, links to the Cape Region are not strong. On the basis of his biogeographical analysis of the African Disinae, Linder (1982) has asserted that the Cape and Afromontane regions comprise a single chorological region. However he noted only two instances of geographical replacement across the Kaffrarian Interval. The quartzites of the Zuurberg range in the S.E. Cape form the eastern boundary of the Cape Region which I recognize as a chorion distinct from, but of equal rank to, the Afromontane Region (Fig. 1; White, 1976a; 1982; Werger, 1978b). A very small proportion (5-10%) of the species of genera centred in the Cape are found north of the Kaffrarian Interval (Weimarck, 1941).

I define CAL elements as those taxa common to both Cape and Afromontane grassland, fynbos and other shrubland communities. CAL elements comprise 7.2% of the Humansdorp sample flora. Typical examples are Cliffortia linearifolia, Erica maesta, Oxalis smithiana, Aspalathus spinosa ssp. spinosa, Graderia scabra, Metalasia muricata, Passerina filifolius, Phylica paniculata, Helichrysum anomalum, H. odoratissimum, Arctotis arctotoides and Geranium incanum.

An interesting distribution pattern is shown by species common to the Cape Region and the T.M.G. sandstone formations of Pondoland and southern Natal (Williams, 1972; Hilliard, 1978; Linder, 1982). Examples from the Humansdorp sample flora are Helichrysum felinum, Disparago ericoides and Passerina vulgaris. It would appear that substrate preferences are of great importance in determining

distributions and the most parsimonious decision would be to regard the species as outliers of the Cape Flora. I classified them as CAL elements.

(vi) Cape-Tongaland-Pondoland linking elements (CTL)

Subtropical Tongaland-Pondoland species extend deep into the Cape Region along the Coastal Forelands, and species of Cape affinity are fairly common on the coastal dune systems of the S.E. Cape, Transkei and Natal coasts (Moll & White, 1978). For taxa to qualify as CTL elements they must grow in communities characteristic of both the Tongaland-Pondoland and Cape regions.

I classified 4.4% of the Humansdorp sample flora as CTL elements. Taxa of tropical-subtropical genera include many species confined or nearly confined to coastal calcareous substrates. Examples are Cassine maritima, Rhus crenata, R. schlechteri, Euclea racemosa ssp. racemosa, Rapanea gilliana, Myrica cordifolia and M. quercifolia. Cape elements which range from the south western Cape to the Natal coast include Passerina rigida, Chironia baccifera and Helichrysum teretifolium.

(vii) Cape-Karoo-Namib linking species (CKL)

There was a small component of species (5.8% of the sample flora) common to the Cape and Karoo-Namib regions. Many of these species occupy the sometimes narrow transitional zone between dry fynbos and karroid communities. On the coastal lowlands of the southern and western Cape the boundary between the Cape and Karoo-Namib regions is often unclear and some mixing of the floras occurs (Werger, 1978a). Other CKL elements occur in dry fynbos, and the karroid communities of the Great Escarpment. Very few CKL elements are widely distributed in the Karoo-Namib Region; most are confined to the Western Cape and Karoo Domains (sensu Werger, 1978a). Examples of CKL elements in the Humansdorp sample flora include Relhania genistaefolia, Eriocephalus africanus, Elytropappus rhinocerotis, Selago corymbosa, Barleria pungens, Lampranthus elegans and Polyxena ensifolia.

(viii) Afromontane-Tongaland-Pondoland linking species (ATL)

The coastal region of Natal, Transkei and the S.E. Cape is the only part of Africa where Afromontane and lowland species intermingle in any number over a relatively extensive area (White, 1978). In this area the lower limit of the Afromontane Region is difficult to define compared with the situation in tropical Africa (Moll &

White, 1978). Tinley (1975) asserts that all evergreen forest south of the Natal-Mozambique border forms part of an "Afrotemperate Biome". Moll and White (1978) emphasize the transitional nature of Tongaland-Pondoland flora.

However the region is rich in endemics (40% of larger woody species are endemic) Moll & White, 1978).

Many Afromontane species are common canopy trees in Tongaland-Pondoland forests. A large group of species grow in both the Tongaland-Pondoland and Afromontane forests of Natal, Transkei and the S.E. Cape and then range inland where they occur in the Afromontane forests of the Transvaal Drakensberg and elsewhere in tropical Africa. Decisions to determine which species are true transgressors are often made with great difficulty and require a good knowledge of species' ecological preferences and patterns of abundance in the two forest types.

ATL elements comprise 7.7% of the Humansdorp sample flora. Examples from the sample flora include Apodytes dimidiata, Teclea natalensis, Cassine tetragona, C. peragua, Canthium inerme, Burchellia bubalina, Ochna arborea, Hippobromus pauciflorus, Linociera foveolata and Rhoicissus tomentosa.

(ix) Tongaland-Pondoland-Karoo-Namib linking species (TKL)

South of the Kei River the Tongaland-Pondoland communities of the river valleys show strong Karoo-Namib links (Moll & White, 1978). A great proportion of the TKL species are succulents endemic to the S.E. Cape river valleys where they occur in both subtropical thicket and karroid communities.

I classified 4.0% of the Humansdorp sample flora as TKL elements. Succulents include Crassula cultrata, C. ovata, C. perforata, Cotyledon velutina, Euphorbia fimbriata, Portulacaria afra and Senecio pyramidatus. Non-succulent and generally more wide ranging species include Schotia afra, Carissa haematocarpa and Lycium austrinum.

(x) Tongaland-Pondoland-Zambezian linking elements (TZL)

North of the Kei river and particularly in the dry inland valleys of Natal, the Tongaland-Pondoland Region shows strong Zambezian links (Moll & White, 1978; Downing & Gibbs Russel, 1981). Very few TZL species occur in the Tongaland-Pondoland thickets of the S.E. Cape. I classified 1.1% of the sample flora as TZL elements. These include Maerua caffra, Euclea natalensis, Plumbago auriculata, Azima tetracantha and Capparis sepiaria.

(xi) Tropical-subtropical wides (TRW)

Many species have limited value in chorological analysis. These include pluriregional transgressor species. In southern Africa there is a large group of species which are widespread in tropical and subtropical phytochoria (including the lower margins of the Afromontane Region) but are absent or poorly represented in the Cape Region and temperate parts of the Karoo-Namib Region. I have grouped these species as TRW elements.

4.1% of the Humansdorp sample flora are TRW species. There are two groups of species: grasses, and trees or shrubs. The grasses include Themeda triandra, Tristachya leucothrix, Eragrostis capensis, Brachiaria serrata and Sporobolus fimbriatus. Some shrub species are Tarchonanthus camphoratus, Cassine aethiopica, Pappea capensis and Euclea crispa.

(xii) Wides (WID)

Wides are pluriregional species distributed throughout most of southern Africa. Many of these species, though widespread in the subcontinent, are restricted to uplands in tropical Africa and are also found in the warm temperate parts of Europe and south western Asia (cf. Burtt, 1971). I included cosmopolitan weeds as WID elements.

WID species comprise 6.6% of the Humansdorp sample flora. Examples are Scabiosa columbaria, Hebenstreitia integrifolia, Senecio burchellii, Hibiscus trionum, Centella coriacea, Bromus japonicus, Briza minor and Helichrysum capillaceum.

b. Endemics and endem centres

I recognized two endem centres in the S.E. Cape, one for Cape taxa, the other for karroid and subtropical taxa. For Cape taxa I used Weimarck's (1941) S.E. Centre (Fig. 1) and for the other species, the Kaffrarian Transition Zone (Fig. 1).

(i) South Eastern Centre

Weimarck (1941) analyzed the distributions of 462 typical Cape taxa and established a system of endem centres and subcentres for the Cape Region. The importance of this pioneering work is often under-estimated. However there are important criticisms of Weimarck's system. The centres are defined exclusively on the distribution of Cape genera and do not stress the importance of ecological

factors and phylogenetic relationships (Nordenstram, 1969). A major criticism is Weimarck's failure to recognize as a single centre the coastal calcrete region of the southern Cape with its rich neo-endemic flora (Dahlgren, 1963; Nordenstram, 1969).

Weimarck (1941) recognized 5 endem centres in the Cape Region including the South Eastern Centre (Fig. 1, Fig. 5). Recent biogeographical analyses of typical Cape genera have not always upheld Weimarck's centres. Williams (1972) and Linder (1982) recognized Western (winter rainfall region) and Southern (bimodal rainfall region) centres for Leucadendron and the Disinae respectively. A numerical analysis of the distributions of 1 936 typical Cape taxa (Oliver, Linder & Rourke, 1982) corroborates some of Weimarck's centres but does not agree with his hierarchy of centres and subcentres.

I have upheld the S.E. Centre for this analysis. 89 taxa or 26.2% of the sample flora CEN component were endemic to this region. For calciophilous dune species I have extended the centre to include the dune coast from George to the Fish River mouth. CEN taxa restricted to the S.E. Centre include Erica pectinifolia, E. demissa, E. unilateralis, Simoechilus barbiger, Gnidia coriacea, Agathosma pilifera, A. puberula, A. acutissima, Protea tenax, Leucadendron loerinse, Passerina pendula, Aspalathus nivea, Phylica abutina and Anapalina intermedia. Calciophilous dune endemics include Agathosma stenopetala, Phylica litoralis, Felicia echinata, Erica chloroloma and Pentaschistis heptamera.

(ii) Kaffrarian Transition Zone

I define the Kaffrarian Transition Zone as incorporating the non-Cape regions of the S.E. Cape. It occupies the lowlands, valleys and inland basins from the Kei to the Gamtoos rivers, and inland to the foothills of the Sneeuwberg-Winterberg-Amatole escarpment. For the subtropical thicket flora the Kaffrarian Transition Zone is a region of transition and floristic impoverishment where a great number of species reach the limits of their distribution ranges. For the karroid succulent flora, however, the zone represents an important endem centre. Endemic succulents from the sample flora include Delosperma echinata, D. ecklonis, Lampranthus productus, Euphorbia fimbriata, E. gorgonis, Gasteria armstrongii, Aloe africana, Senecio pyramidatus and Haworthia fasciata. Non-succulent subtropical trees and shrub endemics are few. The full sample includes Cussonia gamtoensis, Cassine reticulata, Rapanea gilliana and Smelloyphyllum capense.

Statistical analysis

The statistical analysis of the data permits an insight into the static distribution patterns which are essential for both the descriptive and historical approaches to this study. Firstly, I determined for each community in the study area the number of species belonging to the various phytochorological groups and the number of endemics, and expressed these as a percentage of the total community flora. Secondly I performed correlation analyses and stepwise multiple linear regression (Allen & Learn, 1973) using the percentage of species belonging to a phytochorological group and the number of endemics in a given sample plot as the dependent variables and the environmental factors recorded from each plot (Table 4) as the independent variables. I used only those samples with soil fertility data ($n = 97$) in the correlation and regression analyses. Klaus & Frankenberg (1979) have successfully used stepwise multiple linear regression to determine the statistical relationships between phytogeographical groups and climatic factors in the Sahara.

The results of the phytochorological group analysis of the communities are depicted in the phytochorological spectra (cf. Klaus & Frankenberg, 1979) in Fig. 4. It is clear that the full data set can be divided into two groups: Cape Fynbos and Cape Transitional Small-leaved Shrublands which are dominated by CEN and Cape linking elements; and Afromontane Forest and Subtropical Transitional Thicket dominated largely by elements with Afromontane and Tongaland-Pondoland affinities. I therefore performed correlation and regression analyses on these two sets of data independently, as well as on the full data set. In all analyses I used untransformed variables.

ANALYSIS OF PHYTOCHOROLOGICAL PATTERNS AND ENDEMISM

Descriptive approach

In this section I explore the static data base. I discuss the phytochorological spectra for the Humansdorp communities and patterns of endemism in the study area as well as more general patterns in the S.E. Cape. I also examine correlations between the incidence of phytochorological group elements and environmental factors, and isolate environmental variables that can predict the occurrence of phytochorological groups and number of endemics in the study area. I give narrative explanations, concentrating on ecological factors, of present-day phytochorological patterns and endemism.

a. Community chorological patterns and endemism

(i) Phytochorological spectra

Figure 4 shows the phytochorological spectra for each community recognized in the study area. In the Cape Fynbos Shrublands Cape endemics (CEN) dominated the spectra and the remaining species were largely Cape linking elements. The S.E. Mountain Fynbos communities in the study area were composed almost entirely of CEN taxa; there was a minor group showing links to the Afromontane fynbos and grassland communities. These are the "pure" fynbos communities widespread in the south western and southern Cape but restricted in the S.E. Cape to the upper poleward slopes of the higher mountains (Cowling, 1982a).

Grassy Fynbos occurs on sites that are drier and have slightly more fertile soils than mountain fynbos. These communities were characterized by a strong component of Cape-Afromontane linking elements (CAL) indicating links to Afromontane communities and a high incidence of Tropical wides (TRW) which were predominantly tropical-subtropical grasses (Themeda, Heteropogon, Tristachya, etc.). It is probably this floristic component that led Acocks (1953) to assert that fynbos communities of the southern and S.E. Cape are derived in historical times from Afromontane grasslands. The Thamnochortus-Erica community had the strongest CEN component amongst the Grassy Fynbos types, and occurs on highly infertile leached soils (Table 3). The Protea-Clutia community had a similarly high representation of CEN taxa and is found on more fertile colluvial gravels (Table 3). Unlike the other Grassy Fynbos communities which are burnt on a 4-5 year rotation, most stands in the Protea-Clutia sample were unburnt for at least 12 years. Frequent burning of Grassy Fynbos eliminates many obligate reseeding Cape taxa (Cowling, 1982a) and encourages the establishment and growth of C₄ grasses (Cowling, 1982b). The Themeda-Passerina community is restricted to dry areas and had an important Cape-Karoo-Namib linking (CKL) component. The Thamnochortus-Tristachya community is a restioid grassland (*sensu* Campbell et al., 1981) on seasonally waterlogged sands. It is heavily grazed and had many wides (WID), most of which are weedy species.

South Coast Dune Fynbos communities were characterized by the presence of many Cape-Tongaland-Pondoland linking species (CTL). The low incidence of CEN taxa in the Themeda-Stenotaphrum community was because it is bush-cut frequently.

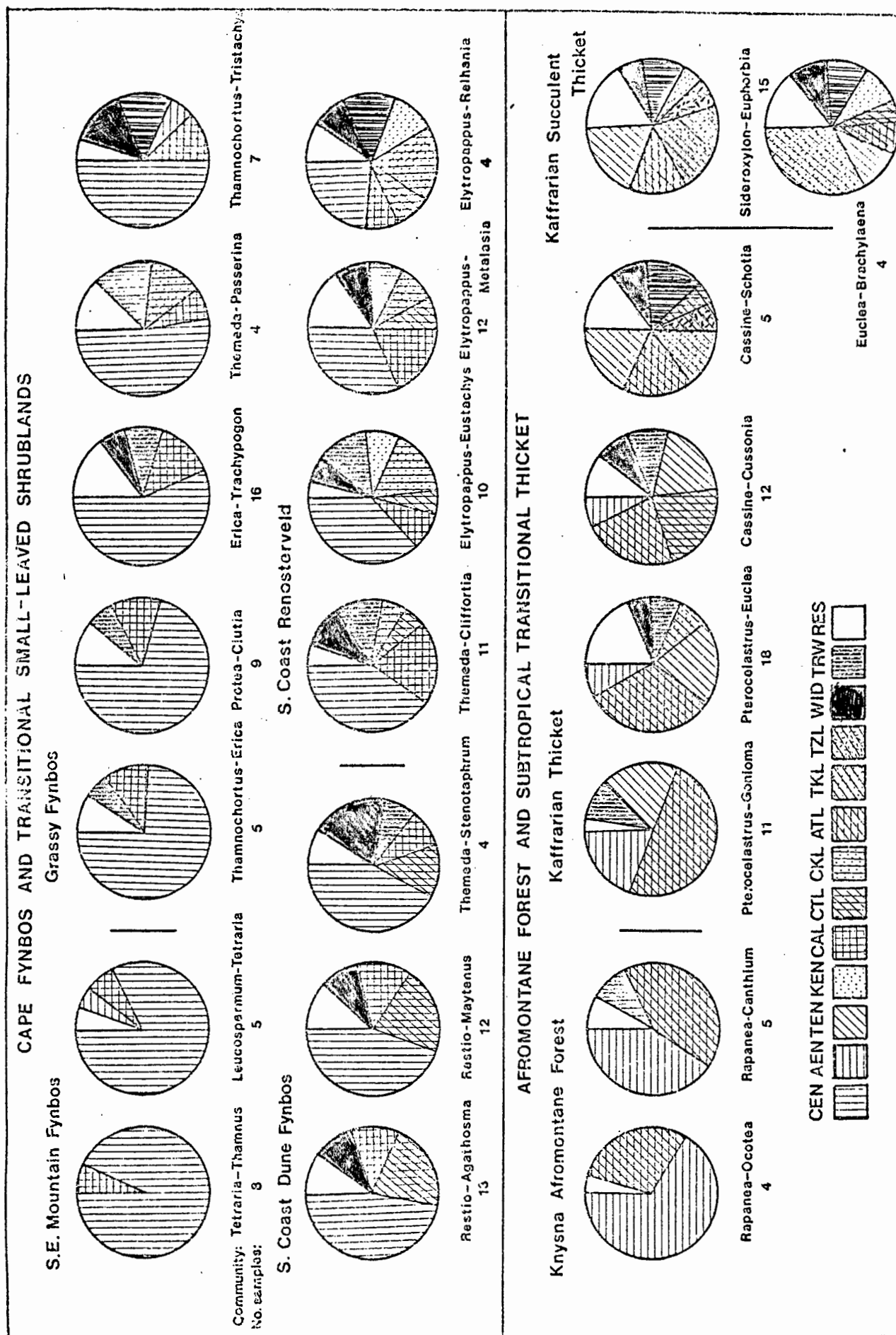


FIG. 4. Phytochemical spectra showing the percentage of species of phytochemical groups within the communities of the study area. CEN = Cape endemics; AEN = Afromontane endemics; TEN = Tongaland-Pondoland endemics; KEN = Karoo-Namib endemics; CAL = Cape-Afromontane linking elements; CTL = Cape-Tongaland-Pondoland; CKL = Cape-Karoo-Namib; ATL = Afromontane-Tongaland-Pondoland; TKL = Tongaland-Pondoland-Karoo-Namib; TZL = Tongaland-Pondoland-Zambezian; WID = wides; TRW = Tropical wides; RES = residual (groups comprising less than 5% of community sample flora and unidentified taxa.)

This practice eliminates fynbos shrubs; however these soon reappear when a stand is not bush-cut for several years. This community had a strong WID component and is also heavily grazed.

Cape Transitional Small-leaved Shrublands, represented in my sample by South Coast Renosterveld communities, had fewer CEN species than Cape Fynbos Shrublands and a predominance of Cape linking elements which indicated their transitional composition. TRW species were well represented. The major shrub species were widely distributed CAL species (e.g. Metalasia muricata, Cliffortia linearifolia, Helichrysum spp.) or CKN species (e.g. Elytropappus rhinocerotis, Relhania genistaefolia). Many of the CEN species were geophytes. Communities found under high rainfall conditions ($500 - 700 \text{ mm yr}^{-1}$; Themeda-Cliffortia, Elytropappus-Metalasia communities) had strong Afromontane affinities while drier communities ($400 - 500 \text{ mm yr}^{-1}$; Elytropappus-Eustachys, Elytropappus-Relhania communities) had strong karroid links.

Afromontane Forest and Subtropical Transitional Thicket communities had strikingly different phytochorological spectra from Cape Fynbos and Transitional Small-leaved shrublands (Fig. 4). The former were overwhelmingly dominated by taxa with Afromontane and Tongaland-Pondoland affinities; Cape elements were almost entirely lacking.

In the Knysna Afromontane Forest communities Afromontane endemics (AEN) predominated and most of the remaining taxa were Afromontane-Tongaland-Pondoland linking elements (ATL). The drier Rapanea-Canthium community which shows affinities to the Subtropical Transitional Forests of the S.E. Cape coast (Alexandria Forest of Acocks (1953)) had a strong ATL component. This analysis supports the assertion by White (1976a; 1978) that the Knysna forest enclave should be included as part of the Afromontane archipelago and not grouped with Coastal Tropical Forest Types (Acocks, 1953) or separated as a Cape "Temperate Forest" (Axelrod & Raven, 1978).

Subtropical Transitional Thicket communities were characterized by a predominance of Tongaland-Pondoland linking species (Fig. 4). Kaffrarian Thicket is a weakly succulent Tongaland-Pondoland thicket to low forest, with strong Afromontane links. The Pterocelastrus-Gonioma community, which is confined to colluvial talus and scree soils derived from T.M.G. quartzites, had the strongest Afromon-

tane affinities. The Cassine-Cussonia community is a mesic dune thicket with a strong CTL component. The Cassine-Schotia community is a dry dune thicket, restricted to the Gamtoos River mouth region and had a spectrum more typical of Kaffrarian Succulent Thicket (Fig. 4).

Kaffrarian Succulent Thicket is a dry thicket type characteristic of the river valleys of the S.E. Cape. The communities have complex phytochorological relationships. They are distinguished from Kaffrarian Thicket by their strong Karoo-Namib links (Fig. 4).

(ii) Endemism

Table 5 shows patterns of endemism in the communities of the study area.

14.6% of the total sample flora was endemic to either the South Eastern Centre or the Kaffrarian Transition Zone. Of these endemics about 70% were of Cape affinity and about 20% karroid; subtropical and Afromontane taxa contributed very little to total endemism. Most of the endemics were shrubs and trees. 17 species, or 13% of the total, were succulents. Of the 31 herbaceous endemics, 58% were geophytes.

When endemics were expressed as a percentage of the community sample flora, highest values were recorded from the fynbos communities, especially S.E. Mountain Fynbos (Table 5). Most of these endemics were Cape shrubs although karroid taxa were common in the drier communities. Amongst the fynbos communities I recorded lowest levels of endemism in the South Coast Dune Fynbos.

Levels of endemism in renosterveld communities were generally lower than fynbos (Table 5). Cape shrubs were poorly represented and karroid taxa comprised almost half the samples of each community. Highest endemism was recorded from the Elytropappus-Eustachys community which differs from other renosterveld communities as it occurs in a dry region near the Gamtoos valley on stony sandy soils derived from Cretaceous conglomerates (Table 3) and is transitional to Grassy Fynbos (Cowling, 1982a). The endemics in this community included certain Cape shrubs (e.g. Passerina pendula, Erica demissa, Agathosma gonaquensis) and karroid succulents (e.g. Haworthia fasciata, Tricodiadema decorum, Lampranthus productus) not found in the other renosterveld communities.

TABLE 5. A comparison of endemism in communities of the study area

Communities	Number of endemics/100m ²		Total endemics in community				Endemics as a % of community sample flora	Geographical affinity (% of total number of endemics)				Number of 100m ² samples
	\bar{X}	S.D.	Shrubs & trees	Herbs	Succulents	Total		Cape	Karoo	Subtropical	Afromontane	
S.E. Mountain Fynbos	5.0	2.1	13	4	0	17	19.5	100	0	0	0	8
Tetradlea-Thamnia	4.0	1.2	11	1	0	12	21.4	100	0	0	0	5
Leucospermum-Tetradlea												
Grassy Fynbos	5.0	2.5	9	1	0	10	14.5	100	0	0	0	5
Thamnochortus-Erica	6.4	2.1	17	2	0	19	14.8	100	0	0	0	9
Protea-Clusia	5.5	2.1	23	4	3	30	14.2	86.7	13.3	0	0	16
Erica-Trachypogon	7.0	2.4	14	1	3	18	19.6	61.1	38.9	0	0	4
Themeda-Paspalum	4.1	1.7	9	4	0	13	9.8	100	0	0	0	7
Themnochortus-Tristachya												
South Coast Dune Fynbos	5.3	2.3	9	9	1	19	13.2	89.4	5.3	5.3	0	13
Restio-Agathosia	4.0	2.6	7	7	1	15	13.2	86.7	0	13.3	0	12
Restio-Maytenus	4.5	2.1	4	6	0	10	9.6	90	0	10	0	4
Themeda-Stenotaphrum												
South Coast Renosterveld	1.4	1.3	1	3	1	5	4.2	40	40	20	0	11
Themeda-Cliffortia	7.4	2.4	12	5	6	23	14.2	39.1	60.9	0	0	10
Elytropappus-Eustachys	2.3	1.6	6	4	2	12	7.8	53.9	46.2	0	0	12
Elytropappus-Metastasia	3.3	1.3	5	8	1	9	9.3	55.6	44.4	0	0	4
Elytropappus-Relbunium												
Knysna Afro-montane Forest	0.5	0.6	0	2	0	2	5.9	0	0	0	100	4
Rapanea-Ocotea	1.0	1.0	1	2	0	3	4.2	0	0	33.3	66.6	5
Rapanea-Canthium												
Kaffrarian Thicket	2.4	1.6	5	2	1	7	6.5	14.3	14.3	42.9	28.6	11
Pterocelastrus-Gonioma	2.2	1.3	4	2	5	11	8.5	0	63.6	18.2	18.2	18
Pterocelastrus-Euclea	0.8	0.6	2	0	3	5	5.4	20	40	40	0	12
Cassine-Cussonia	1.8	1.5	1	0	3	4	6.0	0	50	50	0	5
Cassine-Schottia												
Kaffrarian Succulent Thicket	3.6	2.8	5	3	7	15	12.5	0	66.7	33.3	0	15
Sideroxylon-Euphorbia	4.0	2.2	3	1	6	10	9.3	0	80	20	0	4
Euclea-Brachylaena												
Total sample	3.7	2.6	80	31	17	128	14.6	69.5	21.9	5.5	3.1	194

Among the non-Cape communities I recorded lowest endemism in the Afromontane Forest communities. Within the thicket types the levels of endemism were determined largely by the karroid contribution; highest endemism was recorded in Kaffrarian Succulent Thicket where there was a high incidence of succulent karroid endems. (Table 5).

These results lose much of their interpretative value because of a lack of comparative data. Gibbs Russel & Robinson (1981) present data, for diverse taxa, on percentage endemism in the eastern Cape. Their values range from 1% (trees) to 18% (Crassulaceae) with a mean of 5.4% for all groups combined. They considered the eastern Cape a region of low endemism when compared to rich endem centres such as the Cape Floristic Region (73% of flora endemic) and the Namib Desert (35%).

Figure 5 shows the distribution of 1 142 typical Cape taxa within Weimarck's (1941) endem centres for the Cape Floristic Region. Included in the sample are 462 taxa, from Weimarck's study, including genera in the Restionaceae, Cyperaceae, Iridaceae, Rosaceae, Thymeleaceae, Boraginaceae and Compositae. I analyzed the distributions of a further 680 taxa from nine genera including Adenandria (Strid, 1972), Agathosma (Pillans, 1950), Aspalathus (Dahlgren, 1963), Leucadendron (Williams, 1972), Leucospermum (Rourke, 1972), Muraltia (Levyns, 1954), Paranomus (Levyns, 1970), Sorocephalus (Rourke, 1969) and Spatalla (Rourke, 1969). The data (Fig. 5) illustrates the well documented pattern of a massing of species and high endemism in the south west and a drop-off towards the north and east (cf. Levyns, 1938; 1954; 1964; Dahlgren, 1963; Oliver et al., 1982). However the South Eastern Centre emerges as a relatively rich region with the third highest percentage endemism (27.2%) (Fig. 5).

Table 6 shows patterns of endemism in the S.E. Cape of certain succulent genera, largely of karroid affinity. Most of the S.E. Cape taxa grow in the succulent thicket, dry renosterveld and succulent karoo communities of the river valleys and inland basins. Levels of endemism within many of the genera are very high and it seems that along with the Namaqualand-Richtersveld region of the Cape west coast, and the Little Karoo region of the southern Cape, the S.E. Cape ranks as an important focus of diversity and endem centre for karroid succulents. Croizat (1965) recognized an Albany Centre in the S.E. Cape, based on endems in

TABLE 6. Patterns of endemism¹ of some succulent genera in the south eastern Cape

Taxon	Distribution Centre	No. spp. in genus ²	No. in S.E. Cape	% of total in S.E. Cape	No. endemic to S.E. Cape	% endemism in S.E. Cape	Data source
Crassulaceae							
<u>Cotyledon</u>	Karoo-Namib	9	6	66.7	3	50	Court (1981)
<u>Andromischus</u>	Karoo-Namib	27	7	25.9	7	100	Court (1981)
<u>Crassula</u>	Karoo-Namib	144	51	35.4	5	3.5	Tölken (1977), Court (1981)
Liliaceae (Aloineae)							
<u>Haworthia</u>	Karoo-Namib	67	23	34.3	20	87	Court (1981) Taxonomically problematic
<u>Aloe</u>	Widespread	150	25	16.7	5	20	Reynolds (1950)
<u>Astrolobia</u>	Karoo-Namib	6	4	66.7	2	50	Court (1981)
<u>Chaemaloe</u>	Karoo-Namib	1	1	100	1	100	Court (1981) Monotypic genus from Uitenhage district.
<u>Gasteria</u>	Karoo-Namib	20	13	65	11	84.6	Court (1981) Taxonomically problematic
Euphorbiaceae (Euphorbiaeae)							
<u>Euphorbia</u>	Karoo-Namib	193	44	22.8	36	83.7	White, Dyer & Sloane (1941), Court (1981)
Asclepidaceae (Stapelieae)							
<u>Tridentea</u>	Karoo-Namib	14	3	21.4	2	66.7	Court (1981)
<u>Stapelia</u>	Karoo-Namib	52	9	17.3	7	77.8	Court (1981)
<u>Huernia</u>	Karoo-Namib	43	10	23.3	6	60	Court (1981)
Mesembryanthemoideae:- no specific data available							
Karoo-Namib							
Genera centred in the S.E. Cape: <u>Platythra</u> (monotypic genus in S.E. Cape) <u>Bergeranthus</u>, <u>Rhombophyllum</u>, <u>Faucaria</u>, <u>Orthopterum</u>							
Goldblatt (1978), Court (1981)							

¹ Endemic to Kaffrarian Transition Zone² Southern African species only (R.S.A., Namibia, Lesotho, Swaziland and Botswana)

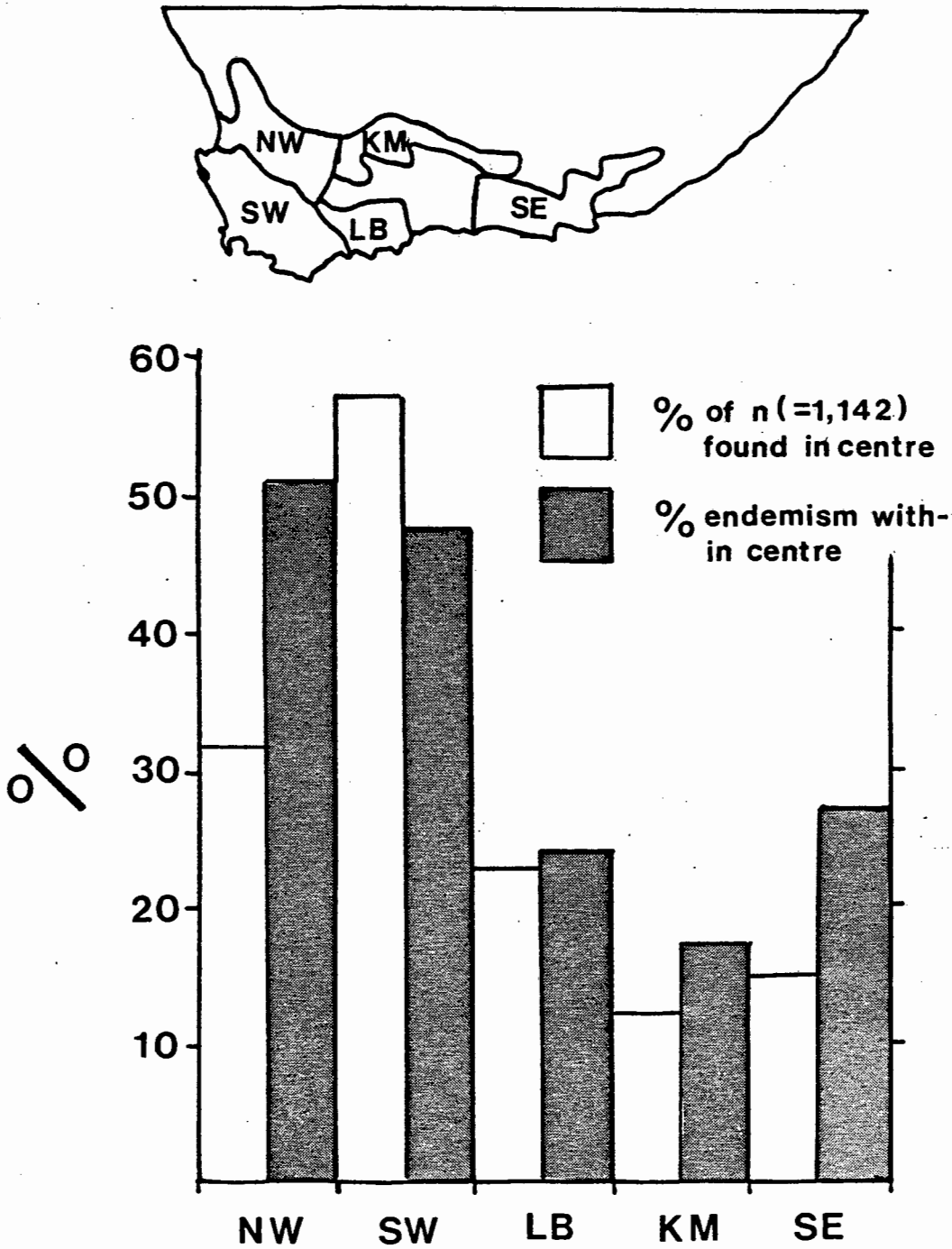


FIG. 5. Location of Weimarck's (1941) endem centres in the Cape Region, and distribution of taxa within the centres. Open columns indicate the percentage of total taxa analyzed ($n = 1\,142$) found in each endem centre. Shaded columns indicate the percentage of within-centre species endemic to a particular centre.

Euphorbia. Other succulent genera well represented by endems in the region are Cotyledon, Haworthia, Gasteria, Bergeranthus and Faucaria (Table 6).

Nordenstram (1969) recognized a very distinct Albany Centre for Euryops, an African genus of 97 species centred in the Cape. Nordenstram states: "In a broader view of South African phytogeography, the Albany Centre stands out as one of the most significant foci". Euryops is a typical component of Cape Transitional Small-leaved Shrublands and Nordenstram (1969) argues that the genus could be regarded as a member of the karoo flora. Passerina, a more typical Cape genus but also characteristic of transitional shrublands in ecotonal situations, has a centre of diversity and endemism in the S.E. Cape (Thoday, 1925). The region is also a centre for certain monocot geophytes including Cyrtanthus (Dyer, 1939), Albuca and Ornithogalum.

There are very few subtropical shrub and tree endemics in the S.E. Cape (cf. Gibbs Russel & Robinson, 1981). In addition to the taxa already noted from the study area, there are a few more species including Encephalartos latifrons, E. princeps, Boscia oleoides, Ozoroa mucronata and Atalaya capensis. When expressed as a percentage of the total subtropical tree and shrub flora in the S.E. Cape, the level of endemism was about 4%. By comparison approximately 18% of the subtropical forest and thicket trees and shrubs were endemic to the Natal-Transkei region (pers. data).

There were only two Afromontane species from the Humansdorp sample flora endemic to the S.E. Cape, and both are herbs of the forest floor. Sterculia alexandri, Sparmannia africana and Strelitzia alba are the only Afromontane trees endemic or nearly endemic to the region. Local endemism is generally poorly developed in Afromontane forest trees (White, 1978).

Although the flora of the S.E. Cape is characterized by wide ranging taxa which have their distribution limits in the region, endemism is not uniformly low as suggested by Gibbs Russel & Robinson (1981). In the western part of the area there was a relatively rich endemic flora of Cape affinity and the dry river valleys were an important endem centre for succulent karroid taxa. There were, however, very few endemics amongst subtropical and Afromontane shrubs and trees and subtropical grasses (Gibbs Russel & Robinson, 1981).

b. Correlation and regression analyses

I have used linear models of correlation and regression on data where the dependent and independent variables may show non-linear polymodal relationships. Thus in many cases the analyses presented here must be regarded as possible underestimates of the true relationships which may exist. A high correlation or well fitting regression does indicate a reasonably linear relation between variables.

(i) Simple correlation analysis

Table 7 presents a matrix of correlation coefficients for the full data set ($n = 97$). Tables 8 and 9 show the independent (environmental) variables with which the percentage frequency of phytochorological groups and number of endemics per 100 m² sample are significantly correlated for the fynbos and renosterveld communities ($n = 64$), and the forest and thicket communities ($n = 33$) respectively. Not surprisingly there are many intercorrelations among the environmental variables (Table 7). In the three analyses there are important differences in the variables explaining the relative frequency of phytochorological groups and number of endemics. I explore these relationships below.

CEN elements showed highly significant negative relationships with vegetation age (VAG) in the full data set analysis (Table 7) and the forest and thicket data subset (Table 9), and a positive relationship with VAG for the fynbos and renosterveld analysis (Table 8). With respect to the first mentioned data sets, CEN elements were associated with fire-prone communities, usually burnt on a 4 to 15 yr rotation (Cowling, 1982b). However when fynbos and renosterveld communities were treated alone the highest frequency of CEN elements was found in more mature vegetation. This is largely because frequent burning often eliminates fire sensitive, obligate reseeding Cape shrubs (Cowling, 1982a). In Table 7 CEN elements showed a positive relationship with grazing intensity since most Grassy Fynbos and renosterveld communities are grazed; Table 8 showed a negative relationship since mountain fynbos, which has the highest proportion of CEN elements, is largely ungrazed. CEN elements were generally associated with shallow stony acid sandy infertile soils with a low litter cover (Tables 7 - 9). In Table 8 their frequency was positively correlated with altitude (ALT), rainfall (RAI) (see also Table 7) and slope (SLO) and negatively correlated with aspect (ASP) indicating a preference for high altitude steep poleward slopes.

TABLE 7. Correlation matrix of environmental variables and phytochorological groups. Only values (Pearson's r) with $P < .01$ are shown. Full data set ($n = 97$). See Table 4 and text for explanation of variable abbreviations.

	VAG	GRZ	RAI	ALT	ASP	SLO	LIT	RCO	SDE	SAN	PHH	CAC	BAS	CAR	NIT	PHO
Independent variables	VAG	1.00														
	GRZ	-.83	1.00													
	RAI			1.00												
	ALT			.49	1.00											
	ASP					1.00										
	SLO	.40	-.38		.32		1.00									
	LIT	.83	-.80			.30	1.00									
	RCO				.29			1.00								
	SDE	.30	-.27					-.58	1.00							
	SAN	-.36		.29			-.24			1.00						
	PHH			-.57			-.40	.42			1.00					
	CAC	.45	-.40	-.34			.35	-.30	.31		.75	1.00				
	BAS	.59	-.47	-.39			.45	-.31			.65	.91	1.00			
	CAR	.51	-.42			.41	.40			-.30		.45	.68	1.00		
	NIT	.59	-.42			.28	.49			-.38		.55	.73	.85	1.00	
	PHO	.31	-.31		-.27		.28		.37		.49	.40	.35			1.00
Dependent variables	CEN	-.73	.44	.37	.33		-.46	.36	-.35	.42	-.36	-.51	-.65	.50	-.65	-.37
	AEN	.42	-.32	.41	.43		.37				-.27			.37	.47	
	TEN	.84	-.68	-.26	-.28		.67	-.32	.36	-.27	.41	.59	.75	.52	.59	.45
	KEN			-.56						-.29						
	CAL	-.72	.71			-.32	.64		.31			-.39	-.44	-.38	-.39	-.27
	CTL			-.44					.29	.29	.64	.31				
	CKL	-.37	.45	-.47			-.43	.34	-.35							
	ATL	.83	-.69			.44	.68	-.26	.31	-.26		.39	.61	.63	.72	
	TKL	.55	-.41	-.50			.41					.35	.33			
	TZL	.48	-.39	-.43			.39				.43	.36				.38
	WID		.34	-.35				-.34			.39					
	TRW			-.42			-.42			-.31						
	END	-.31			-.29			.32		.31			-.29	-.26	-.39	

TABLE 8. Environmental variables with which phytochorological groups are correlated with $P < .05$. Values in table are Pearson's r . Fynbos and renosterveld communities ($n = 64$). See Table 4 and text for explanation of variable abbreviations

Variables	Dependent									
	CEN	TEN	KEN	CAL	CTL	CKL	ATL	WID	TRW	END
Independent										
VAG	.59			-.29				-.46	-.49	
GRZ	-.46			.40		.32		.43	.52	
RAI	.50		-.58	-.32		-.69			-.47	
ALT	.62			-.36	-.47			-.38	-.31	
ASP	-.32						.30		.36	-.36
SLO	.31						.28	-.30	-.29	
LIT	.56			-.27		-.33		-.42	-.47	
RCO	.24		.42		-.28	.27		-.44		.26
SDE		.38			.39	-.27	.25	.42		
SAN	.29		-.24	-.42		-.37			-.39	.41
PHH	-.40	.47			.75		.34	.48		
CAC	-.39	.49			.73		.46	.36		
BAS	-.52	.47			.71		.53	.31		
CAR	-.31	.30			.27		.55			
NIT	-.55	.38			.43		.60			-.31
PHO	-.32	.65			.63		.52	.39		

Because of their poor representation in fynbos and renosterveld communities (Fig. 4) I did not include the AEN group in the analysis of that data set (Table 8). The contribution of AEN species was positively correlated with VAG and negatively correlated with GRZ (Table 7) as this group was commonly found in forest and thicket which are not fire-prone vegetation types and are seldom grazed (Cowling, 1982a). The relative frequency of the AEN group was positively correlated with ALT, RAI, total soil nitrogen (NIT), soil litter (LIT), organic carbon (CAR) and negatively correlated with soil pH (PHH), showing a preference for acid, nitrogen- and organic-rich soils.

The TEN group showed relationships which are the inverse of CEN elements. In all data sets (Tables 7 - 9) the relative frequency of this group was positively correlated with measures of soil fertility and soil depth (SDE). These relationships were most pronounced in Tables 7 and 8. Within the full spectrum of communities sampled (Table 7) TEN elements were positively correlated with VAG, LIT and negatively correlated with rock cover (RCO), GRZ, RAI and ALT (see also Table 9).

RAI emerged as the factor showing strong negative relationships with the KEN group in all three analyses. There were negative correlations with soil sand content in Tables 7 and 8.

CAL elements were largely absent from forest and thicket communities (Fig. 4) and were not included in the analysis of that data set.

The occurrence of the CAL group was correlated with a similar suite of environmental variables to the CEN group (Table 7). However the former group was more strongly associated with GRZ and showed positive relationships with SDE and LIT and a negative relationship with SLO. There were weaker negative relationships with soil fertility factors and no relationship with pH. When the fynbos and renosterveld communities were analyzed as a data subset (Table 8) it was clear that the CAL group was associated with lower rainfall and lower altitude sites and less sandy soils. Other soil factors were non-correlated.

In the full data set (Table 7) the relative frequency of CTL species was negatively correlated with ALT and positively correlated with SDE, SAN, PHH and exchangeable calcium (CAC) indicating a preference for deep calcareous coastal dune sands (cf. Fig. 4). In the fynbos and renosterveld communities (Table 8) all measures of soil fertility were positively correlated with the CTL group showing a preference for

the more fertile sites within the spectrum of soils sampled. In the forest and thicket communities (Table 9) only SAN and PHH amongst the soil variables, were positively correlated with CTL while negative relationships were shown with VAG, probably because CTL species were best represented in the less mature dune thickets.

The CKL group was not considered for analysis in the forest and thicket community data subset (cf. Fig. 4). Along with the CEN and CAL groups, this group was associated with fire-prone and grazed systems. The most significant relationships were negative correlations with RAI. The CKL group also showed negative correlations with LIT and SAN and positive correlations with RCO (Tables 7 and 8).

The ATL group showed many relationships similar to the TEN group. In the full data set (Table 7) ATL species were associated with mature ungrazed sites with deep, non-rocky fertile soils. In the fynbos and renosterveld communities (Table 8) it was clear that the more fertile soils favoured ATL species whereas in the thicket and forest communities (Table 9) RAI, NIT and soil organic carbon (CAR) emerged as factors showing strong positive correlations.

Because of their low occurrence in fynbos and renosterveld communities I have not considered the TKL and TZL in the analysis of that data set (cf. Fig. 4). Like the other predominantly thicket groups both the TKL and the TZL groups were positively correlated with VAG and negatively correlated with GRZ (Table 7). Both groups showed negative relationships with RAI indicating a preference for dry thicket, and positive relationships with certain measures of soil fertility. When the thicket and forest communities were treated alone, RAI emerged as a factor showing strong negative relations with both groups (Table 9).

The WID group did not show very strong relationships with environmental variables and these relationships varied greatly in the different data sets. In the full data set (Table 7) the group was positively correlated with GRZ and PHH and negatively correlated with RAI and RCO. In the fynbos and renosterveld communities (Table 8) WID species were associated with grazed and burnt vegetation on low altitude level sites with deep, relatively fertile, non-rocky soils. In the forest and thicket communities (Table 9) the WID group was most strongly associated with drier low altitude sites with a lower litter cover.

In the full data set the TRW group was negatively correlated with RAI, LIT and SAN (Table 7). In the fynbos and renosterveld data set (Table 8), where most TRW species are subtropical C₄ grasses, there were clearer relationships with environmental variables. Here the abundance of TRW species was greatest in immature vegetation on low altitude, low rainfall, level sites; grazed sites with equatorward aspects and low litter cover and soil sand content were favoured. These relationships indicate a preference for lowland renosterveld communities. In the forest and thicket communities (Table 9) relationships with the TRW group were obscure: there was a strong positive correlation with available soil phosphorus (PHO) and a weaker positive relationship with SLO.

Endemics (END) expressed as the number of taxa per 100 m² sample, showed a tendency to increase in sandier, rockier and less fertile soils; they also showed negative correlations with VAG and ALT indicating a preference for fire-prone, low altitude situations (Table 7). In the fynbos and renosterveld communities (Table 8) END was positively correlated with RCO and SAN and negatively correlated with NIT and ASP. END showed positive relationships with CEN ($r = .26, P > .05$) and CAL ($r = .25, P > .05$). These relationships indicated a tendency for endem abundance to be associated with fynbos communities on infertile soils. In the forest and thicket communities (Table 9) the only factor to emerge with a significant (negative) relationship with END was RAI. END showed strong positive relationships with KEN ($r = .61, P > .001$) and TKL ($r = .801, P < .001$) showing a strong association with the drier thicket communities with karroid affinities.

These results showed that there were two important classes of phytochorological groups, as reflected in their ecological relationships. The first class was characteristic of fire-prone shrublands which are variously grazed by domestic livestock. These include the CEN, CAL and CKL groups which predominated in fynbos and renosterveld communities (Fig. 4). Shallow rocky sandy infertile soils were important in explaining the abundance of CEN elements, to a lesser degree of CAL elements and not at all of CKL elements. The latter two groups were most prevalent on lowland sites while the CKL group was most abundant in regions of relatively low rainfall.

The second class comprised those groups characteristic of vegetation which was neither grazed nor fire-prone. It includes the AEN, TEN, ATL, TKL and TZL groups which typified forest and thicket (Fig. 4), and occurred on deeper more fertile soils than the fynbos and renosterveld groups. The TEN, TZL and especially the TKL groups occurred in dry conditions relative to the AEN and ATL groups. These last two mentioned groups were strongly associated with soils rich in organic carbon and nitrogen.

The remaining groups do not fit into the classes described above. KEN elements were strongly associated with low rainfall conditions in both renosterveld/fynbos and forest/thicket communities. CTL elements were well represented in both dune fynbos and thicket communities and therefore showed no significant relationships with VAG or GRZ. Most of the variance in their relative frequency was explained by the substrate characteristics of the calcareous dune sands. The WID group was generally associated with heavily grazed situations on the more fertile lowland soils and the TRW group, at least in the fynbos and renosterveld communities, was most abundant on warmer lowland sites with moderately fertile soils.

(ii) Multiple linear regression analysis

In this section I isolate the environmental factors which can predict the relative frequency of the phytochorological groups and the number of endemics in a 100 m² sample. The regression models for the full data set, the fynbos and renosterveld communities and the thicket and forest communities are shown in Tables 10, 11 and 12 respectively. The tables show the first three independent variables, chosen by forward selection (Draper & Smith, 1966) at a specified significance of $P < .05$. Where fewer than three factors provided that level of fit, only the factors with an acceptable fit are listed. The maximum variance (R^2) accounted for by all independent variables entering the model at $P < .05$ is also shown. An analysis of the residuals showed that the assumptions of normality of the residuals and homogeneity of variances were satisfied for all models in the regressions.

For the full data set (Table 10) 13 out of the 16 environmental factors emerged as predictors. The measured factors which did not prove good predictors were CAC, PHO and the sum of exchangeable bases (BAS). The maximum R^2 accounted for by the regressions varied from 25 to 87%. There were well-fitting regressions for the CEN (80% of variance), TEN (86%) and ATL (87%) groups and poor fits for the END (25%), TRW (36%) and WID (38%) groups. VAG emerged as a strong

TABLE 10. Multiple linear regression models for dependence of the relative importance of phytochorological groups on the first three environmental variables chosen by forward selection. See Table 4 and text for explanation of variable abbreviations. Analysis of full data set ($n = 97$)

Phytochorological group	Independent variables	Regression coefficients (b_i)	Intercept	R^2	Maximum R^2 (specified, $P < .05$)	F ratio
CEN	VAG	-1.5353	69.51	.53	.80	105.50
	ALT	.0690		.65		88.97
	GRZ	-8.802		.72		78.43
AEN	NIT	62.0156	-6.24	.22	.62	26.68
	ALT	.0308		.47		41.54
	BAS	-.5258		.52		33.97
TEN	VAG	.2936	-1.04	.71	.86	233.60
	BAS	.2876		.81		199.26
	ALT	-.0125		.84		161.21
KEN	RAI	-.0199	12.73	.31	.43	42.91
	ALT	.0075		.35		25.87
	SDE	.9630		.38		18.68
CAL	VAG	-.2924	25.30	.52	.63	104.73
	SAN	-.1242		.60		70.39
	ALT	-.0084		.63		51.69
CTL	PHH	4.7022	-17.33	.41	.52	65.11
	VAG	-.1309		.47		42.24
	SLO	.2592		.50		30.82
CKL	RAI	-.0174	16.71	.22	.51	26.61
	LIT	-.0715		.41		32.26
	RCO	.0643		.47		27.40
ATL	VAG	.4759	-16.12	.70	.87	219.20
	NIT	35.6398		.78		162.48
	RAI	.0152		.79		118.91
TKL	VAG	.2257	15.53	.31	.65	45.78
	RAI	-.0218		.49		41.72
	NIT	-14.7691		.55		38.56
TZL	VAG	.0433	4.23	.23	.56	28.85
	RAI	-.0067		.38		28.42
	PHO	.0388		.42		22.87
WID	PHH	1.6642	-3.92	.15	.38	17.21
	GRZ	1.6190		.33		23.46
	RCO	-.0610		.38		19.09
TRW	RAI	-.0145	26.98	.18	.36	20.68
	SAN	-.0836		.36		12.87
	SLO	-.2242		.37		10.42
END	NIT	-6.3849	4.58	.15	.25	17.2
	RCO	.0338		.22		13.5
	ASP	-.1804		.25		10.3

TABLE 11. Multiple linear regression models for dependence of the relative importance of phytochorological groups on the first three environmental variables chosen by forward selection.
See Table 4 and text for explanation of variable abbreviations.
Analysis of fynbos and renosterveld communities (n = 64)

Phytochorological group	Independent variables	Regression coefficients (b _j)	Intercept	R ²	Maximum R ² (specified, P < .05)	F ratio
CEN	ALT	.0456	49.19	.38	.76	38.59
	NIT	-.92.0194		.50		30.16
	LIT	.3787		.61		31.32
TEN	PHO	.1471	-1.68	.42	.56	44.96
	NIT	7.6844		.49		28.91
	LIT	.0180		.51		20.88
KEN	RAI	-.0150	9.24	.34	.51	32.14
	RCO	.0534		.41		21.6
	SDE	1.5280		.46		17.02
CAL	SAN	-.1803	20.72	.17	.45	12.78
	ALT	-.0120		.28		11.89
	RAI	.0139		.33		9.94
CTL	PHH	4.5104	-17.13	.56	.64	78.98
	SLO	.5546		.60		45.11
	ALT	-.0159		.64		35.77
CKL	RAI	-.0354	32.05	.48	.53	57.09
	SAN	-.0600		.51		31.45
	ALT	.0071		.53		22.55
ATL	NIT	25.50	-5.20	.36	.64	35.10
	PHO	.1831		.53		33.90
	SLO	.2768		.61		30.81
WID	PHH	2.0180	-10.18	.23	.48	18.86
	GRZ	2.2753		.43		23.42
	SDE	2.4941		.48		18.10
TRW	GRZ	2.1238	10.24	.27	.56	23.01
	ASP	.8389		.38		19.05
	RAI	-.0162		.47		17.97
END	SAN	.0569	.59			12.62
	ASP	-.3171				9.72
	RCO	.0289				8.95

TABLE 12. Multiple linear regression models for dependence of the relative importance of phytochorological groups on the first three environmental variables chosen by forward selection. See Table 4 and text for explanation of variable abbreviations. Analysis of thicket and forest communities ($n = 33$)

Phytochorological group	Independent variables	Regression coefficients (b_i)	Intercept	R^2	Maximum R^2 (specified $P < .05$)	F ratio
CEN	VAG	-.3360	22.21	.35	.53	16.49
	LIT	-.0656		.53		16.58
AEN	ALT	.0666	-40.22	.70	.91	72.31
	RAI	.0510		.84		76.48
	LIT	.1768		.88		69.29
TEN	ALT	-.0300	-10.28	.43	.70	23.72
	VAG	.5372		.59		21.73
	BAS	.2609		.67		19.37
KEN	RAI	-.0203	13.58	.26	.35	10.88
	ALT	.0112		.35		8.13
CTL	VAG	-1.3035	74.22	.67	.80	63.68
	ALT	-.0176		.74		41.62
	PHO	-.0836		.77		23.60
ATL	RAI	.0471	-4.34	.27	.77	11.17
	NIT	24.5117		.36		8.44
	ALT	-.0289		.44		7.49
TKL	RAI	-.0553	65.01	.49	.82	29.35
	PHH	-3.4871		.56		19.25
	RCO	-.4793		.68		20.26
TZL	RAI	-.0187	13.95	.44	.56	24.36
	RCO	-.1220		.49		14.54
	ALT	.0075		.56		12.26
WID	RAI	-.0103	17.66	.17	.33	6.57
	LIT	-.0760		.33		7.51
TRW	PHO	.1717	7.79	.30	.30	13.04
END	RAI	-.0104	12.82	.35	.61	17.08
	PHH	-.6000		.52		16.44
	PHO	-.8324		.61		15.40

independent predictor of group importance, distinguishing between groups characteristic of fynbos and renosterveld (negative coefficients) and thicket and forest (positive coefficients). Although no two groups appeared to be affected by the same set of factors, measures of soil fertility commonly predicted the percentage of taxa in groups characteristic of thicket and forest communities. The incidence of KEN species and karroid linking species (CKL, TKL) was strongly predicted by RAI. NIT was an important predictor of END.

In the fynbos and renosterveld communities (Table 11) no single model accounted for less than 45% of the variance. VAG was not an important independent predictor. ~~Measures of soil fertility~~ Measures of soil fertility were important predictors of fynbos (negative coefficients) and thicket (positive coefficients) groups. NIT was selected as the chief independent predictor of the incidence of CEN taxa.

Table 12 presents the regression models for the thicket and forest communities. There were well fitting models for the AEN (91% of variance), CTL (80%) and TKL (82%) models.

Historical approach

For a full understanding of biogeographic patterns it is not possible to separate the effects of ecological and historical factors (Vuilleumier & Simberloff, 1980). To generate biogeographical hypotheses one needs an understanding of the nature, amplitude and timing of paleoenvironmental changes. Climatic change, for example, introduces non-equilibrium states which profoundly affect the predictions made by biogeographic theories based solely on ecological parameters (Livingstone, 1975). An important part of an historical approach is the phylogenetic analysis of taxa emphasizing the cladistic component, and also the analysis of vicariance, speciation and endemism. In this section I review briefly palaeoenvironmental change in the Cape coastal region and discuss the available data on phylogeny and speciation of taxa in the S.E. Cape as an historical input to the formulation of biogeographic hypotheses to be presented below.

a. Palaeoenvironments and vegetation change

In this brief review I focus on environmental and associated vegetation changes in the last glacial maximum of the Upper Pleistocene (18 000 b.p.) to Holocene sequence in the Cape coastal region. I do this largely because there is a more complete palaeoenvironmental record for this period than any other time but also because it was an extremely important period in the evolution and diversification of the present day flora in the region (Rourke, 1972; Axelrod & Raven, 1978; Goldblatt, 1978; Deacon, 1982a).

The present climate of the subcontinent is controlled by the behaviour of the subtropical anticyclones over the South Atlantic and Indian Oceans. The essentially modern circulation patterns probably date from the end of the Miocene when the Antarctic ice sheet was accumulating (Tankard & Rogers, 1978). The onset of summer dry conditions in the south western Cape probably dates from the Plio-Pleistocene with the advent of an approximately present-day location and intensity of the South Atlantic anticyclone and a strengthening of the cold Benguela current (Tankard & Rogers, 1978; Deacon 1982a). Largely on the basis of the herbivore fossil record from sites on the south western Cape lowlands (cf. Hendey, 1973) Tankard and Rogers (1978) postdict a progressive desiccation from the Miocene through the Plio-Pleistocene.

Recent evidence from diverse sources and disciplines indicates that Pleistocene climatic changes were more complex than previously assumed (Deacon, 1982b). Pleistocene climatic patterns have been largely determined by the successive decay of continental ice sheets in Eurasia and North America which has resulted in a series of globally synchronous glacials and interglacials. Van Zinderen Bakker (1976) made a bold attempt to model glacial-interglacial climates in the Cape coastal region. Assuming a 10° northward displacement of the Antarctic Polar Front, Van Zinderen Bakker (1976) suggested a glacial climate with colder "pluvial" conditions resulting from a greater penetration of cyclonic rains into the subcontinent. Evidence for a lower glacial temperature (approximately 5°C along the Cape coast) is adduced from frost weathered screes, block streams and block fields on the Cape Folded Belt (Butzer & Helgren, 1972; Deacon, 1982b) and cryoclastic weathering of cave deposits along the southern Cape coast (Butzer, 1973). Further evidence for low glacial temperatures comes from an analysis of faunal remains in southern

Cape caves (Klein, 1980) which indicate open, possibly C₃ grasslands in regions which presently support thicket and forest vegetation.

Van Zinderen Bakker's (1976) model has been explicitly followed by several workers including Livingstone (1975), Tankard & Rogers (1978) and Axelrod & Raven (1978). These authors cite the forest expansion on the Cape Flats near Cape Town (Schalke, 1973) as evidence for wetter glacial conditions. However, the only reliable date for forest growth on the Cape Flats is the period 45 000 to 40 500 b.p. which coincides with a warmer interstadial (Coetzee, 1978; Deacon, 1982a) and not a cold period as suggested by Schalke (1973). Axelrod & Raven (1978) assert that fynbos was severely limited within its present area by the expansion of temperate forest during the most recent "pluvial" cycle. They postdict that ... "at such a time sclerophyllous vegetation (fynbos) must have shifted northward, into the present Namib and a good part of the western karoo ... " and that "the sclerophyllous Cape flora was largely swept into its present area as the dry climate expanded following the last pluvial ... ". There is no evidence to suggest that fynbos ever migrated en masse from its mountain stronghold during the last glacial (Deacon, 1982a). My data indicated that fynbos elements were strongly bound to the infertile substrates peculiar to the mountains of the Cape Folded Belt (see also Taylor, 1978; 1980; Kruger, 1979). It is conceivable that under wetter conditions certain taxa would migrate from the mountains onto the more fertile substrates of the coastal forelands and intermontane valleys. I argue that this migration would be limited to a minor component of generalist species. The low fertility of the mountain substrates would not have prevented the expansion of forests as fynbos and Afromontane Forest communities occur on similarly impoverished soils today (Van Daalen, 1980). Necessary requirements for forest expansion on the mountains would have been deeper, moisture-retaining soils and a relatively mild climate with an adequate moisture supply throughout the year. There is some evidence of deeper palaeosols in the southern Cape mountains (W. Bond, pers. comm.) but new evidence presented below on glacial climates clearly militates against extensive forest expansion.

It appears that there is no acceptable sequence of pluvials in southern Africa (Deacon, 1982a). Recent studies indicate that the belt of westerlies was not displaced more than the order of 10° northward at the last glacial maximum relative to the present (Lancaster, 1979; Deacon, 1982b). There is much evidence to suggest that the last glacial was considerably drier (and colder) in the Cape coastal region than the present (Nicholson & Flohn, 1980; Deacon, 1982a; 1982b). A recent study of the micromammals in the deposits of the Boomplaas Cave, located in a southern Cape intermontane valley indicates a high proportion of dry habitat karroid species during the last glacial (Avery, 1979). Palynological data from the same site show a predominance of Compositae (Stoebe or Elytropappus?) in the last glacial and a more mesic and diversified flora including thicket, grass and fynbos species in the Holocene (H. Deacon, pers. comm.). Identified charcoals from cave deposits in the same area show an increase in subtropical thicket species (Diospyros/Euclea, Maytenus/Pterocelastrus) since 13 000 b.p. with a peak in percentage frequencies between 8 000 and 6 000 b.p.; a massive increase in Acacia karoo charcoals is recorded after about 5 000 b.p. (Deacon, 1978; Opperman, 1978; H. Deacon, pers. comm.). In the Knysna district Martin (1968) has shown that relatively dry conditions prevailed prior to 7 000 b.p.

From these data it is possible to infer a glacial-interglacial scenario for the Cape coastal region of cold and dry glacial conditions followed by a warmer wetter interglacial (Deacon, 1982a; 1982b). Unfortunately the amplitude of these climatic changes is not quantified and cannot be generalized to a broad spectrum of habitats, thus undermining their value in predicting associated vegetation changes. If, during the last glacial, the ocean was colder along the southern and S.E. Cape coasts (cf. Vincent, 1972; McIntyre, 1977 in Coetzee, 1978; CLIMAP, 1976) the amount of post-frontal precipitation, benefitting largely the river valleys and intermontane basins, may have been drastically reduced, since moist air would have been advected over a cooler ocean. Glacial rainfall patterns would have varied considerably with topography as the interior low lying country would benefit less from the cyclonic rains than the mountains. It is also difficult to untangle the effects of moisture and temperature: lower glacial temperatures would have meant lower evapotranspiration but this effect may have been partly offset by increased wind velocities (cf. Van Zinderen Bakker, 1976).

In the Cape coastal region Pleistocene climatic modelling must still make great advances before models can be used to predict accurately changes in the region's biota. However the refutation of the pluvial hypothesis has opened up a new perspective on Pleistocene climates in South Africa (Deacon, 1982b).

b. Phylogeny speciation and endemism

In this section I attempt to give direction to the distribution tracks by investigating the available data on phylogenies, vicariance, speciation and endemism in an historical perspective. My efforts have been largely frustrated by a lack of data. Unfortunately most South African plant taxonomists have espoused no particular systematic or evolutionary principles so that one can deduce very little concerning the comparative distribution of primitive or derived taxa (cf. Ball, 1976).

A notable exception is the recent work by Linder (1982) on the Disinae. I cannot overstress the importance of cladistic hypotheses in systematic studies; it is possible to deduce from these hypotheses predictions which can be tested using independent lines of evidence and can then be incorporated as ancillary evidence for more general biogeographic theories.

(i) Cape taxa

The complex topography of the Cape Folded Mountains, in conjunction with climatic changes, has undoubtedly promoted allopatric or geographic speciation (Grant, 1971) of Cape taxa (Goldblatt, 1978). Allopatric speciation has been noted by Levyns (1954), Rourke (1972) and Bremer (1976) for plants and by Barnard (1936) for "ground beetles" (Colophon). Linder (1982) finds little evidence for allopatric speciation of the Cape Disinae. He suggests differential selection along ecological gradients as an important factor promoting speciation in this group. This implies in situ radiation, as highly localized ecological conditions are of great importance (Linder, 1982).

There have been few studies on vicariance in Cape taxa. Vicariads within the primitive Crassicaudex section of Leucospermum indicate an early Tertiary migration into the Cape from the north east (Rourke, 1972; see also Levyns, 1954 for Muraltia). The results of a cladistic analysis of the Disinae by Linder (1982) suggest a Cape origin for the group, followed by a migration northwards into East and West Africa.

A striking feature of typical Cape taxa is the high concentration of narrow endemics which are invariably restricted to the acid infertile soils of the mountains and the alkaline calcareous soils of the coastal lowlands while far fewer endemics are recorded from the more fertile lowland soils (Levyns, 1954; Dahlgren, 1968; Rourke, 1972; Williams, 1972; Oliver *et al.*, 1982; Table 5). Highly localized endemics are often associated with peculiar substrates elsewhere, such as norite, pyroxenite, serpentine and chrome seams of the Great Dyke in Zimbabwe (Wild, 1968), serpentine outcrops and other ultrabasic rocks in North America (Mason, 1946), infertile quartzites in the Chimanimani mountains, Zimbabwe (Wild, 1964) and in Natal and Transkei (Hilliard, 1978; Van Wyk & Lötter, 1982).

Wild (1964; 1968) argues that areas of peculiar substrate constitute island-like situations within continental land masses, because of edaphic barriers to plant migrations. He cites evidence from the Chimanimani mountains in eastern Zimbabwe where 4.6% of the total flora of the mountain complex is endemic to the infertile soils derived from the Pre Cambrian quartzites (Wild, 1964). Further evidence is from ultrabasic soils of central Zimbabwe where nearly 7% of the tolerant species are confined to these substrates (Wild, 1968).

The edaphic-island theory has important implications for the Cape Region. Campbell (1982) has demonstrated a gradient, from the western to the eastern Cape, of increasing fertility in the T.M.G. derived soils. There is a parallel decrease along this gradient of the numbers of typical Cape taxa and levels of endemism (Fig. 5). I propose that this is largely because of a partial breakdown of the edaphic barrier in the eastern fynbos region, resulting in an intermingling of Cape taxa with elements from adjacent phytochoria. This chorological complexity is seen in the S.E. Cape Grassy Fynbos communities but not in the S.E. Mountain Fynbos (Fig. 4) on less fertile soils; the latter communities also have the highest levels of endemism.

This discussion can only highlight gaps in our knowledge regarding phylogenies and modes of speciation in the Cape Flora. There is a need to evaluate critically the relevance to the Cape Flora of theories associating speciation with peculiar edaphic conditions (cf. Raven, 1964). Perhaps the role of large-scale allopatric speciation has been overemphasized since current evidence indicates that gene exchange is limited to very small populations within a given species (Ehrlich & Raven, 1969).

(ii) Karroid taxa

There has been a massive diversification of succulent taxa in the southern and south western part of the Karoo-Namib Region (Werger, 1978a). An understanding of the richness of the Cape Region will not be achieved without a knowledge of the evolution and speciation within the Mesembryanthemaceae, Stapelieae and genera such as Crassula and Euphorbia. Regrettably there are few data and in many groups the taxonomy is still highly problematic.

The semi arid river valleys and inland basins of the S.E. Cape comprise an endem centre and focus of richness for many succulent karroid taxa (Table 6). The existence of both endemic monotypic genera (Table 6) and of recent hybridization and numerous neoendemics (e.g. in Euphorbia (White, Dyer & Sloan, 1941)) testifies to a relatively ancient centre of succulent karroid taxa in the S.E. Cape.

Without cladistic phytogeographic analyses it is not really possible to infer migration pathways for karroid taxa. There are indications of a possible recent southwards migration of subtropical arborescent euphorbias into the S.E. Cape. Crossing and recrossing of E. coerulescens (a karroid form endemic to the S.E. Cape) with E. triangularis and E. tetragona (subtropical tree forms) in the Fish River valley has resulted in a hybrid crowd loosely grouped as the E. bothae complex (White et al., 1941). Within the strictly karroid taxa the principal migratory pathways would have been along the major river valleys.

(iii) Subtropical taxa

The subtropical flora in the S.E. Cape is characterized by wide ranging species, most of which reach their limits of distribution in the region. The flora is comprised mainly of trees, shrubs and C₄ grasses.

In the woody taxa of subtropical affinity, endemic to the S.E. Cape or elsewhere in the Cape Region, there appears to have been an evolution of shrub-like descendants from tropical-subtropical arborescent ancestors. A similar pattern is shown in the evolution, from pachycaul ancestors, of geoxylic suffrutices on infertile seasonally waterlogged sandy soils in the Zambezian Region (White, 1976b). Rapanea gilliana is a low shrub with thick "rhizomes" capable of producing aerial stems along their length; it is largely confined to seasonally waterlogged dune sands in the S.E. Cape and appears to be closely related to the arborescent R. melanophloeos. A species with a similar growth form is Olea exasperata which is restricted to

coastal dune sands of the Cape Region and the south western Tongaland-Pondoland Region, and is phylogenetically akin to the taller and more widely distributed Olea europae ssp. africana (= Olea africana) (Verdoorn, 1963). Maytenus lucida is a low shrub confined to the dune systems of the S.W. Cape; it is derived from M. procumbens (Robson, 1966) a Tongaland-Pondoland tree or tall shrub. Cussonia gamtooiensis, a 3-4 m tree confined to the succulent thicket of the lower Gamtoos and Baviaanskloof river valleys, appears to be a recent derivative from the C. spicata complex (Strey, 1981).

Geographical variation and isolation have played an important role in the diversification of tropical and subtropical thicket taxa (White, 1962). A high frequency of eco-geographic replacement indicates a relatively recent diversification.

Within the Euclea racemosa complex F. White (pers. comm.) recognized seven geographical subspecies. Four of these are found in the S.E. Cape and the most derived form (ssp. racemosa) extends as far as the western Cape coastal forelands.

The few data available indicate a small-scale, relatively recent diversification of subtropical shrub taxa in the S.E. Cape comprising largely the CTL elements described above. The migration pathway appears to have come from the more richly diversified flora to the north east. With the possible exception of Smellophyllum a monotypic genus confined to mesic thickets and dry Afromontane Forests in the S.E. Cape, there are no putative subtropical paleoendemics in the region.

(iv) Afromontane taxa

There are few Afromontane Forest species endemic to the southern and S.E. Cape; levels of endemism amongst Afromontane grassland and fynbos taxa are also low.

In my scheme, endems of the latter group restricted to fynbos and allied communities in the S.E. Cape, would be classified as CEN taxa. There are, however, only three species which would be included in this group. Local endemism among Afromontane grassland and fynbos taxa can be quite high (Wild, 1964; Hilliard, 1978; Linder, 1982) but never equals that of Cape fynbos species. There is evidence of a two-way interchange of taxa between the Cape and Afromontane regions (CAL elements) (Hilliard, 1978; Linder, 1982) but the direction of this distribution track for different taxa is difficult to determine. It is unfortunate that Hilliard (1978) did not present evidence on supraspecific distribution tracks for the Natal Compositae.

South African Afromontane Forests (Drakensberg System of White, 1978) are depauperate relative to the tropical African systems but have a higher percentage of local endemics (White, 1978). However these "local" endemics have extensive ranges: e.g. Sclopia mundii - 4 800 km; Cunonia capensis - 1 700 km. There appears to have been little recent diversification and most endemics are probably relictual.

(v) A speciation scenario for the S.E. Cape

Recently Gibbs Russel & Robinson (1981) have presented a speciation scenario for the eastern Cape. In their analysis they followed the work of Stebbins (1974) who argues that tension zones of high ecological diversity (climate, topography, soil) where species are at the limits of their distribution, should be regions favourable for active speciation and the production of youthful endemics (see also Stebbins & Major, 1965; Hopper, 1979). Gibbs Russel & Robinson (1981) therefore predicted high endemism for the eastern Cape since it fulfils the tension zone requirements. However they did not record the expected high level of endemism in the region.

To explain their observations Gibbs Russel & Robinson (1981) proposed that since the eastern Cape is a convergence zone of several phytochoria, each with floras having distinct evolutionary histories, there will always be generalist genotypes to fill niches which may result from environmental change. They view the eastern Cape as a repository for genetically diverse weedy species recruited from different phytochoria depending on the prevailing climatic conditions. Under drier conditions there would be an invasion of karroid generalists (e.g. Pteronia incana, Chrysocoma tenuifolia, Elytropappus rhinocerotis and Felicia filifolia) whereas wetter conditions would favour a dominance by subtropical (Themeda triandra, Acacia karroo) and Cape (Cliffortia linearifolia) generalists.

Gibbs Russel & Robinson's (1981) hypothesis has much merit. It can be tested by examining more widely in the eastern Cape the phytochorological affinities and endemism in communities and also the genotypic variability of major invasive species. Although palynological studies cannot usually detect the specific composition of palaeocommunities they can be of value in determining community-type turnover in response to climatic change. Gibbs Russel & Robinson's (1981) hypothesis predicts fairly gross compositional changes in eastern Cape vegetation as a result of relatively minor climatic changes.

My data showed that endemism in the communities of the Humansdorp study area was not universally low; relatively high endemism was recorded for fynbos taxa on infertile substrates and karroid taxa of the dry river valleys (Table 5). It is possible that Gibbs Russel & Robinson's (1981) model applies largely to the planed topography of the eastern Cape coastal forelands and interfluves and not the Cape Folded Mountains with their substrate-specific fynbos flora and the arid river valleys which have provided refugia for a rich karroid flora. The Kalahari-Highveld Transition Zone (Werger and Coetzee, 1978; White, 1982) is in many respects similar to the eastern Cape as it comprises a tension zone where the Karoo-Namib, Afromontane and Zambezian region intergrade. The region occupies level terrain and is characterized by a generalist flora with few endems (White, 1982).

VEGETATION HISTORY IN THE S.E. CAPE: HYPOTHESES

In this section I propose explanations of vegetation history in the S.E. Cape and, where possible, generalize these for the Cape Region and elsewhere in southern Africa. I focus on the period since the last glacial maximum (18 000 b.p.) to illustrate a hypothetical scenario in a Pleistocene glacial-interglacial sequence. My explanations draw on diverse lines of evidence including the ecological factors governing the distributions of phyto-chorological groups, paleoclimatic data, phylogenetic histories and patterns of speciation and endemism. Implicit in these explanations is the assumption that the overall floristic structure of the major plant assemblages and the ecological factors determining their distribution have not differed drastically in the last glacial to Holocene sequence. I try to give some test implications of the hypotheses I develop.

Cape Fynbos Shrublands

At the outset I wish to dissolve the myth that the southern and S.E. Cape fynbos communities are derived, as a result of agricultural malpractices in historical times, from Afromontane forest and grassland (Acocks, 1953). This theory has been explicitly accepted by Axelrod & Raven (1978) who state: "The fynbos ... has greatly expanded its area to the eastward into areas of summer rainfall in the past 500 years." Martin (1966) and Cowling (1982a) provide ecological arguments to refute Acocks' assertion. Certainly the high endemism recorded for S.E. Cape fynbos vegetation (Table 5, Fig. 5) indicates that fynbos has had a lengthy history in the region.

I argue that the Cape fynbos flora has been largely restricted to an edaphic island comprising the mountains of the Cape Folded Belt and that the flora was never displaced from this region. Levyns (1950) contends that in the southern and S.E. Cape the distribution of fynbos is determined not by edaphic factors but by soil moisture. She bases her argument on the distribution of fynbos, renosterveld and succulent karroid communities on four koppies along a rainfall gradient in the southern Cape (Levyns, 1950). She states: "The lithological characters of the four kopjes appear to be somewhat similar and it is improbable that the features of the vegetation ... are due to differences in soil." She provided no data on soil fertility from different aspects on the four koppies. The geology of the koppies is Witteberg quartzite and Bokkeveld shale which, in the southern and S.E. Cape weather into moderately fertile soils where rainfall and even aspect can have important effects on the leaching régime. My data indicated that CEN taxa are strongly associated with sandy infertile soils (Tables 7 - 9).

Cooler and drier glacial conditions would have restricted mountain fynbos vegetation in the S.E. Cape to the uppermost peaks of the higher mountains where orographic effects would have compensated for the general reduction in rainfall. On the more fertile lowland soils which presently support Grassy Fynbos there would have been an intermingling of fynbos, karroid taxa, and C₃ temperate grasses. With the onset of warmer wetter conditions in the Holocene, mountain fynbos communities would have expanded due to greater leaching of lowland T.M.G. soils. Subtropical C₄ grasses and Afromontane (CAL) elements would have penetrated into the warmer lowland communities on more fertile soils, resulting in the present day Grassy Fynbos.

There is a further, though rather vague hypothesis, that xeromorphic features such as sclerophylly and small leaf size which are associated with infertile soils (Beadle, 1966; Small, 1973) would have pre-adapted the fynbos flora to withstand drier paleoclimates, thus resulting in relatively few extinctions and a possible proliferation on infertile soils in the growing areas of semi-aridity. Hopper (1979) argues this case for heath flora on infertile soils in south western Australia. It is feasible to envisage that Pleistocene climatic fluctuations would not generally have disrupted the distribution of fynbos vegetation on the infertile substrates of the Cape Folded Belt but "merely resulted in changes of community composition, no doubt isolating species' sub-populations in some cases, but not causing excessive extinction ..." (Kruger & Taylor, 1979). A long uninterrupted history of a

fynbos flora in the Cape Region with frequent pulses of speciation within different taxa would explain the enormous richness and high endemism of the flora.

There has been a secondary centre of diversification of Cape taxa on the alkaline substrates of the coastal forelands. Many of the calciophilous endems have vicariads on the adjacent quartzite substrates (Levyns, 1954; Dahlgren, 1963; 1968; Rourke, 1972) suggesting a Pleistocene or post Pleistocene speciation (Rourke, 1972).

The hypotheses presented above have certain testable predictions. The $^{13}\text{C}/^{12}\text{C}$ ratio in the fossil bones of grazers can be used to test the timing of the invasion of subtropical C_4 grasses in the S.E. Cape (cf. Vogel, 1978). An analysis of vicariance and the phylogenies of Cape taxa on the relatively low quartzite hills of the Albany Zuurberg in the S.E. Cape (see Fig. 1) would be a useful test for the edaphic island theory. The soils derived from the Witteberg quartzites which comprise the range are amongst the most fertile of the Cape Folded Belt quartzitic substrates (B. Campbell, pers. comm.) I would predict, therefore, that during the dry glacial, fynbos would have been almost entirely eliminated from that region. Subsequent invasion from the west would have only occurred in the Holocene so that endemism would be low and any endemics would be recently evolved species with western vicariads. Palynological studies would also test the hypothesis that fynbos would not have been displaced in the Pleistocene and Holocene from the infertile mountain substrates.

Cape Transitional Small-leaved Shrublands

Transitional Small-leaved Shrublands occupy tension zones between adjacent phytochoria: between the Cape and Karoo-Namib regions but also between these and the Afromontane and Tongaland-Pondoland regions (Fig. 6). They are often dominated by one or two species such as Elytropappus rhinocerotis, Metalasia muricata, Relhania spp. and Euryops spp. These species are widely distributed, are able to grow under a wide range of conditions and have "weedy" characteristics (Levyns, 1956; Trollope, 1970). They are mostly derived from Cape taxa. Elytropappus is a Cape genus of six species: five have fairly localized distributions while E. rhinocerotis is widely distributed throughout the Cape region, the Great Escarpment of the south central Cape and parts of the eastern Cape (Levyns, 1927; 1950). Similarly Metalasia is a Cape genus of 33 species, most of which have restricted distributions in the Cape Region (Pillans, 1954). M. muricata is a wide-ranging "weedy" species common in certain Transitional Small-leaved Shrublands (Cowling, 1982a).

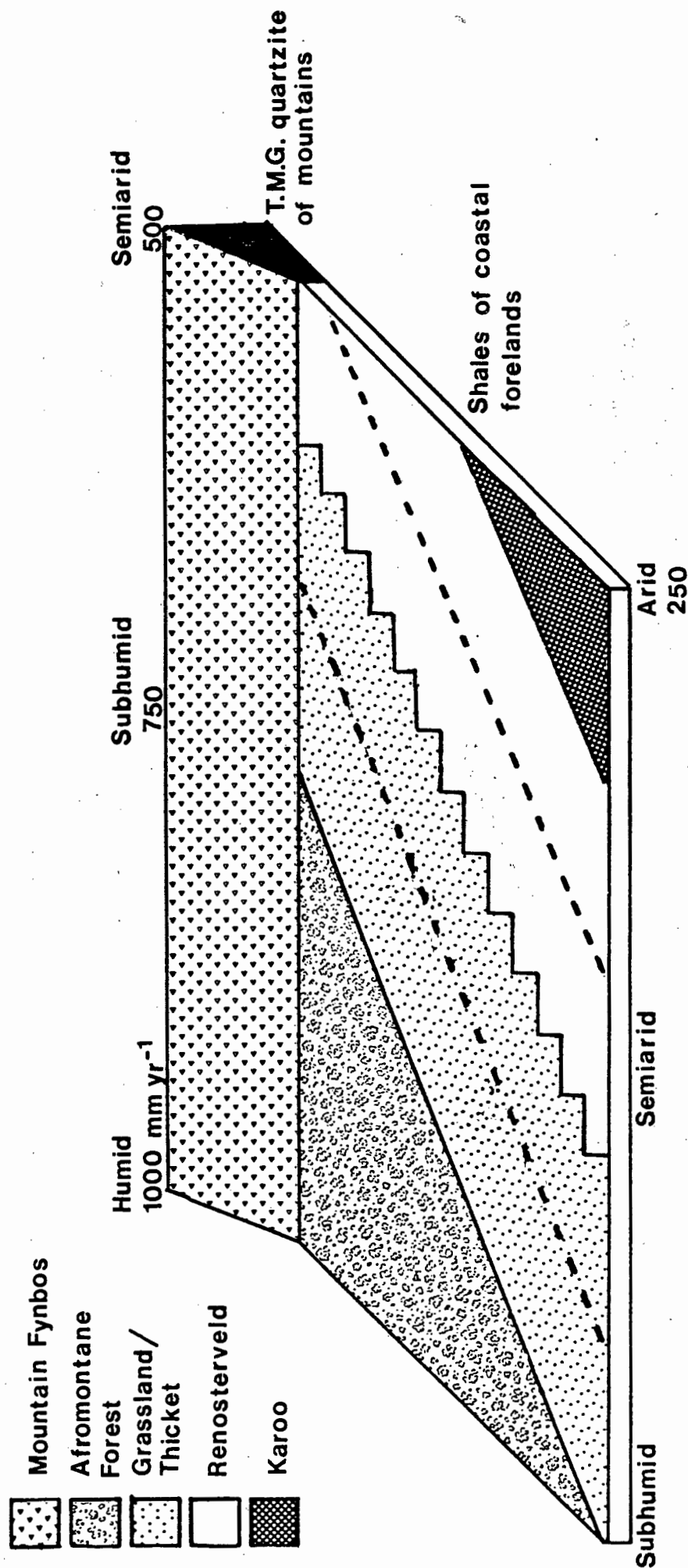


FIG. 6. Renosterveld on the south coast forelands as a tension zone vegetation. Renosterveld communities occupy a zone between karoo and grassland/thicket. The location of this zone would change with climatic fluctuations, and disappear under arid conditions when karoo reached the T.M.G./shale junction. Dashed lines define a sensitive zone vulnerable to mismanagement and the establishment of "false" shrublands (see text).

I present here an hypothesis to explain the origin of Cape Transitional Small-leaved Shrublands. Implicit in this thesis is the assumption that the junction between more fertile soils of the Cape coastal foreland and intermontane valleys and the sandy infertile soils of the Cape Folded Mountains formed an effective migration barrier under most climatic conditions (the edaphic island theory). Extreme climatic differences between the mountains and lowland would reinforce this effect.

The tension zone occupied by Transitional Small-leaved Shrublands would have been unstable during Pleistocene climatic fluctuations. During the last glacial, when conditions were drier than present, the expansion of karroid shrublands on the coastal forelands would have eliminated the Transitional Small-leaved Shrublands in places; in other more mesic regions the Transitional Small-leaved Shrublands would have expanded at the expense of grassland and thicket/forest (Fig. 6).

The instability of this tension zone would have favoured the establishment of weedy shrub species recruited from adjacent phytochoria (cf. Gibbs Russel & Robinson, 1981) explaining the transitional composition and low endemism of shrubs in these communities (Fig. 4, Table 5). In drier regions marginal to karroid shrublands, Transitional Small-leaved Shrublands are regarded as "natural" communities (Acocks, 1953). I suggest that as aridification proceeded and many mesophytic taxa (e.g. subtropical C₄ grasses) were eliminated, E. rhinocerotis and a few other generalist shrubs would occupy their niches, prior to the invasion of karoo. In moister regions where Transitional Small-leaved Shrublands are marginal to grasslands of tropical affinity, man-induced disturbances have telescoped these events by creating environments which are effectively more arid and by minimizing competition through the selective utilization of species by domestic livestock (Fig. 6). In this way South Coast Renosterveld has been derived in historical times from Themeda triandra dominated grasslands (Cowling, 1982a).

The hypothesis I have presented has certain testable predictions. Palynological studies such as those being undertaken by Deacon and associates in the southern Cape (e.g. Deacon, 1979) will be of value in determining the historical sequence of vegetation types.

Demographic studies to determine the population strategies of the major shrub species and an investigation of their genotypic variability may explain the competitive "superiority" of these species under certain conditions. Another factor which could explain the competitive fitness of these species is allelopathy: Squires and Trollope (1979) have clearly demonstrated the allelopathic effects of Chrysocoma tenuifolia, a major invasive

species in false karroid shrublands and a component of drier Transitional Small-leaved Shrublands.

Subtropical Transitional Thicket

The woody and graminoid component of the thicket and succulent thicket communities is largely of tropical affinity. During the last glacial this component would not have withstood the generally colder and drier conditions in the Cape coastal region. Some thickets may have survived in locally moist sites but they would have been composed largely of Afromontane species. With the establishment of warmer wetter conditions after about 12 000 b.p. subtropical thicket species would have migrated into the Cape Region from the north east. They became established on lowland sites with deep well-drained fertile soils. Bimodal and winter rainfall régimes meant that only those species with long-lived sclerophyllous leaves (Sideroxylon, Euclea, Cassine, Diospyros) were capable of penetrating the Cape Region. For subtropical plants growing under these climatic conditions "high cost-slow profit" leaves (Orians and Solbrig, 1977) would be favoured as the plants would be capable of utilizing soil moisture whenever its availability coincides with other optimum growth conditions. The lower proportion of annual precipitation falling in the summer growing season, south of the Kei River, may be an important constraint on the south westward migration of tropical winter deciduous thicket elements (e.g. Acacia, Dichrostachys, Combretum).

The karroid component of the succulent thicket comprises an endem-rich, diverse flora which has probably had a lengthy history in the S.E. Cape. The karroid succulent taxa are largely confined to dry valley sites. During the last glacial these regions would have been drier and the rainfall more erratic than at present. Glacial valley environments would be cool with considerable diurnal temperature ranges due to temperature inversions (Deacon, 1982a). These regions could have been ideal environments for CAM succulents. Work on certain CAM species indicates that dark CO₂ fixation is enhanced by low night temperatures (Kluge & Ting, 1979). Low and erratic rainfall would favour the competitive growth of shallow rooted CAM species (Kluge & Ting, 1979). It is possible, therefore, that karroid succulent species were more widespread in the S.E. Cape river valleys during the last glacial. With the onset of a warmer wetter climate in the Holocene, thicket taxa became established in the valley sites and, in combination with newly evolving succulent species, formed the present-day succulent thicket communities.

Evidence for a Holocene establishment of thicket in the Cape Region comes from palynological and charcoal studies (Opperman, 1978; Deacon, 1979; H. Deacon, pers. comm.) and a strong browsing component in deposits (Klein, 1980), from southern Cape cave sites. It would be of great interest to undertake a palynological study of deposits from suitable valley sites in the S.E. Cape.

Afromontane Forest

In the Cape Region Afromontane Forests are today confined to sites where soil moisture is not limiting for extended periods at any time of the year. They are largely restricted to the poleward aspects of the coastal mountains on colluvial, deep-soil sites which are fed by stream discharge and run-off from adjacent slopes. The incidence of orographic rain is a major factor in determining the distribution of these forests and explains their prevalence on the coastal mountains and the moist Knysna enclave.

There is some evidence that Afromontane Forest in the southern Cape was largely eliminated during drier climatic phases in the Pleistocene. Pleistocene eolian sands of the southern Cape Coastal Platform could only have been deposited when the vegetation was considerably more open than the present day Knysna Afromontane Forest (Butzer & Helgren, 1972). Martin (1968) in a study of pollen bearing deposits from the same region, found evidence for the spread of forest only after about 7 000 b.p. I suggest that during the cold dry glacial, Afromontane forests were virtually eliminated from the Cape Region except for relic stands in more mesic microenvironments. During the Holocene recruitment would have come from the north east where Afromontane Forests probably displaced Tongaland-Pondoland forests in glacial times. This hypothesis, therefore, predicts a relatively recent expansion of forests in the Cape and counters the notion that these forests are entirely relictual. It would be instructive to test this hypothesis by analyzing suitable pollen bearing sediments.

CONCLUDING REMARKS

The generalized hypotheses emergent from this study are summarized as follows:

- (i) The Cape fynbos flora is confined to an island maintained by edaphic barriers; the flora was never displaced from this island stronghold during Pleistocene climatic fluctuations, although certain generalist taxa did migrate onto the more fertile substrates of the adjacent coastal forelands and intermontane valleys. In the S.E.

Cape, where soils are more fertile than other fynbos regions, this barrier has been partially broken down allowing for an intermingling of fynbos with elements from adjacent phytochoria.

- (ii) Cape Transitional Shrublands are unstable tension zone communities whose distribution would have fluctuated dramatically as a result of Pleistocene climatic fluctuations. Their flora indicates that these shrublands have acted as a repository of weedy elements from adjacent phytochoria.
- (iii) Karroid elements, particularly succulents, have had a lengthy history in the coastal regions of the S.E. Cape and have partially been replaced by subtropical and Cape taxa only since the amelioration of the climate in the Holocene.
- (iv) Subtropical thicket and grassland, and Afromontane Forests were almost entirely displaced from the Cape Region during the last glacial and have become established on certain sites in the area, with the onset of a warmer, wetter Holocene climate.

A reconstruction of vegetation history requires a multi-disciplinary approach drawing on diverse lines of evidence. I stand criticized for not addressing the role of pollination and dispersal in determining speciation patterns and the direction of distribution tracks.

Generally, data are lacking for the Cape Region. A significant development in this field is the recent discovery by Bond and Slingsby (1982) that the seeds of 78 plant genera found in fynbos communities are dispersed by ants. Avian dispersal of fruits produced by subtropical shrub species is undoubtedly implicated in thicket migration (Tinley, 1977). More information is required on palaeosol structure and distribution - how different are present-day mountain soils from those of the past?

A further point of criticism is that the conclusions I draw from my analysis of endemism assume roughly equivalent rates of speciation amongst diverse groups of taxa. Wild (1964) found that evolutionary divergence varied within different genera of the Chimanimani flora (see also Hedberg, 1957). It may be true that a comparison of endemism between, for example, subtropical trees and karroid succulent dwarf shrubs is not realistic due to inherent different rates of speciation.

The evidence I have used to formulate the hypotheses on vegetation history is fairly crude. There is, to date, only a qualitative outline of a model for Pleistocene climates in the Cape coastal region. Relevant systematic data and data on modes of speciation and patterns of endemism are glaringly few. Some progress is being made with palaeo -

biological studies but more information is needed. What is required is an entirely deductive approach where data on vegetation history can be tested against predictions made from a reconstruction of palaeoclimates (cf. Deacon, 1982a).

REFERENCES

- Acocks, J.P.H. (1953) Veld types of South Africa. Mem. Bot. Surv. S. Afr. 28.
- Allen, J & Learn, J. (1973) STEPREG 1: Stepwise linear regression analysis.
Reference manual. Academic Computing Centre, Madison.
- Anon. (1942) Weather on the coasts of Southern Africa. Volume 2(3). From Mossel Bay to East London. Government Printer, Pretoria.
- Aweto, A.O. (1981) Organic matter build-up in fallow soil in part of south western Nigeria and its effects on soil properties. J. Biogeogr. 8, 67 - 74.
- Avery, D.M. (1979) Upper Pleistocene and Holocene palaeoenvironments in the southern Cape: the micromammalian evidence from archaeological sites.
Unpublished D. Phil. thesis, University of Stellenbosch.
- Axelrod, D.I. & Raven, P.H. (1978) Late Cretaceous and Tertiary vegetation history of Africa. Biogeography and ecology of southern Africa. (Ed. by M.J.A. Werger) pp. 77 - 130. Junk, The Hague.
- Ball, I.R. (1976) Nature and formulation of biogeographic hypotheses. Syst. Zool. 24, 407 - 430.
- Barnard, K.H. (1936) Geographical zoology. S. Afr. Geogr. J. 14, 3 - 13.
- Beadle, N.C.W. (1966) Soil phosphate and its role in molding segments of the Australian flora and vegetation, with special reference to xeromorphy and sclerophylly. Ecology 47, 992 - 1007.
- Beard, J.S. (1959) The origin of African Proteaceae. Jl. S. Afr. Bot. 25, 231 - 235.
- Bolus, H., (1905). Sketch of the floral regions of South Africa. Science in South Africa (Ed. by W. Flint & J.D.F. Chilchrist), pp.198 - 240. Maskew Miller, Cape Town.
- Bond, W. & Slingsby, P. (1982) Seed dispersal by ants in Cape shrublands, South Africa. Unpublished Ms.
- Boucher, C. & Moll, E.J. (1980) South African mediterranean shrublands. Mediterranean-type shrublands. Ecosystems of the world, vol. 11. (Ed. by F. Di Castri, D.W. Goodall & R.L. Specht), pp. 233 - 248. Elsevier, Amsterdam.
- Brady, N.C. (1974) The nature and properties of soils, 8th edn. Macmillan, New York.

- Bremer, K. (1976) The genus Relhania. Opera Botanica 40, 1 - 85.
- Burtt, B.L., (1971) From the south: an African view of the floras of western Asia. Plant life of South West Asia (Ed. by P.H. Davis), pp. 135 - 154. Botanical Society of Edinburgh, Edinburgh.
- Butzer, K.W. (1978) Geology of Nelson Bay Cave, Robberg, South Africa. S. Afr. Archeol. Bull. 28, 97 - 110.
- Butzer, K.W. & Helgren, D.M. (1972) Late Cainozoic evolution of the Cape coast between Knysna and Cape St. Francis, South Africa. Quart. Res. 2, 143 - 169.
- Campbell, B.M. (1982) Plant environments of the mountains of the Fynbos Biome. Bothalia (in press).
- Campbell, B.M., Cowling, R.M., Bond, W.J. & Kruger, F.J. (1981) Structural characterization of vegetation of the Fynbos Biome. S. Afr. Nat. Sci. Progr. Rep. No. 52, C S I R, Pretoria.
- Clayton, W.D. (1976) The chorology of African mountain grasses. Kew Bulletin 31, 273 - 288.
- CLIMAP. (1976) The surface of the ice age earth. Science, 1131 - 1137.
- Coates Palgrave, K. (1977) Trees of southern Africa. Struik, Cape Town.
- Coetzee, J.A. (1978) Late Cainozoic palaeoenvironments of southern Africa. Antarctic glacial history and world palaeoenvironments (Ed. by E.M. van Zinderen Bakker), pp. 115 - 127. Balkema, Rotterdam.
- Compton, R.H. (1929) The flora of the karoo. S. Afr. J. Sci. 26, 160 - 165.
- Court, D. (1981) Succulent flora of southern Africa. Balkema, Cape Town.
- Cowling, R.M. (1982a) A syntaxonomic and synecological study in the Humansdorp region of the Fynbos Biome. Unpublished Ms.
- Cowling, R.M. (1982b) The occurrence of C₃ and C₄ grasses in fynbos and allied shrublands in the south eastern Cape, South Africa. Unpublished Ms.
- Croizat, L. (1962) Space, time, form: the biological synthesis. Published by the author, Caracas.
- Croizat, L. (1965) An introduction to the subgeneric classification of Euphorbia L. with a stress on the South African and Malagasy species. Webbia 20, 573 - 706.
- Croizat, L., Nelson, G. & Rosen, D.E. (1974) Centers of origin and related concepts. Syst. Zool. 23, 265 - 287.

- Dahlgren, R. (1963). Studies on Aspalathus: phytogeographical aspects.
Bot. Not. 116, 431 - 472.
- Dahlgren, R. (1968). Distribution and substrate in the South African genus Aspalathus.
Bot. Not. 121, 505 - 534.
- Deacon, H.J. (1979) Excavation at Boomplaas Cave - a sequence through the Upper Pleistocene and Holocene in South Africa. World Archaeology 10, 241 - 257.
- Deacon, H.J. (1982a) The comparative evolution of mediterranean-type ecosystems: a southern perspective. Mediterranean-type ecosystems. The role of nutrients (Ed. by F.J. Kruger, D.T. Mitchell & J.U.M. Jarvis). Springer-Verlag, Berlin, Heidelberg, New York (in press).
- Deacon, H.J. (1982b) Another look at the Pleistocene climates of South Africa. Unpublished Ms.
- Downing, B.H. & Gibbs Russel, G.E. (1981) Phytogeographic and biotic relationships of a savanna in southern Africa: analysis of an Angiosperm check-list from Acacia woodland in Zululand. Jl. S. Afr. Bot. 47, 721 - 742.
- Draper, N.R. & Smith H. (1966) Applied regression analysis. John Wiley & Sons, New York.
- Du Toit, A.L. (1966) The geology of South Africa, 3rd edn. Oliver & Boyd, London.
- Dyer, R.A. (1939) A revision of the genus Cyrtanthus. Herbertia 6, 65 - 104.
- Ehrlich, P.R. & Raven, P.H. (1969). Differentiation of populations. Science 165, 1228 - 1231.
- Fourcade, H.G. (1941) Check-list of the flowering plants of the divisions of George, Knysna, Humansdorp, and Uniondale. Mem. Bot. Surv. S. Afr. 20.
- Gibbs Russel, G.E. & Robinson, E.R. (1981) Phytogeography and speciation in the vegetation of the eastern Cape. Bothalia 13, 467 - 472.
- Goldblatt, P. (1978) An analysis of the flora of southern Africa; its characteristics relationships and origins. Ann. Missouri Bot. Gard. 65, 369 - 436.
- Good, R. (1974) The geography of flowering plants. Longmans, London.
- Grant, V. (1971) Plant speciation. Columbia University Press, New York.
- Haughton, S.H., Frommurze, H.F. & Visser, D.J.L. (1937) The geology of portions of the coastal belt near the Gamtoos Valley, Cape Province. Geological Survey Report 151, Government Printer, Pretoria.
- Hedberg, O. (1957) Afroalpine vascular plants. Symb. Bot. Ups. 15, 1 - 411.

- Hendey, Q.B. (1973) Fossil occurrences at Langebaanweg, Cape Province. Nature 244, 13 - 14.
- Heydorn, A.E.F. & Tinley, K.L. (1980) Estuaries of the Cape. Part 1. Synopsis of the Cape coast. C S I R Research Report 380, C S I R, Pretoria.
- Hilliard, O.M. (1978) The geographical distribution of Compositae native to Natal. Notes roy. Bot. Gard. Edinburgh 36, 407 - 425.
- Hopper, S.D. (1979) Biogeographical aspects of speciation in the southwest Australian flora. Ann. Rev. Ecol. Syst. 10, 399 - 422.
- Jackson, S.P. & Tyson, P.D. (1971) Aspects of weather and climate over southern Africa. Environmental Studies Occasional Paper 6, 1 - 11.
- Killick, D.J.B. (1963) An account of the plant ecology of the Cathedral Peak area of the Natal Drakensberg. Mem. Bot. Surv. S. Afr. 34.
- Killick, D.J.B. (1979) African mountain heathlands. Heathlands and related shrublands of the world. A. Descriptive studies. Ecosystems of the world, vol. 9. (Ed. by R.L. Specht), pp.97 - 116. Elsevier, Amsterdam.
- King, L.C. (1972) The coastal plain of southern Africa. Its form, deposits and development. Z. Geomorph. N.F. 16, 239 - 251.
- King, L.C. (1978) The geomorphology of central and southern Africa. Biogeography and ecology of southern Africa (Ed. by M.J.A. Werger), pp. 1 - 17, Junk, The Hague.
- Klaus, D. & Frankenberg, P. (1979) Statistical relationships between floristic composition and mean climatic conditions in the Sahara. J. Biogeogr. 6, 391 - 405.
- Klein, R.G. (1980) Environmental and ecological implications of large mammals from Upper Pleistocene and Holocene sites in southern Africa. Ann. S. Afr. Mus. 81, 223 - 283.
- Kluge, M. & Ting, I.P. (1978) Crassulacean acid metabolism. Analysis of an ecological adaptation. Springer Verlag, Berlin.
- Kruger, F.J. (1979) South African heathlands. Heathlands and related shrublands of the world. A. Descriptive studies. Ecosystems of the world, vol. 9. (Ed. by R.L. Specht), pp. 19 - 80. Elsevier, Amsterdam.
- Kruger, F.J. & Taylor, H.C. (1979) Plant species diversity in Cape fynbos: gamma and delta diversity. Vegetatio 41, 85 - 93.

- Lancaster, I.N. (1979) Evidence for a widespread Late Pleistocene humid period in the Kalahari. Nature 279, 145 - 146.
- Lee, K.E. & Wood, T.G. (1971) Termites and soils. Academic Press, London.
- Levy, M.R. (1927) A revision of Elytropappus. Jl. S. Afr. Bot. 1, 89 - 103.
- Levy, M.R. (1938) Some evidence bearing on the past history of the Cape flora. Trans. roy. Soc. S. Afr. 26, 401 - 424.
- Levy, M.R. (1950) The relations of the Cape and Karoo floras near Ladismith, Cape. Trans. roy. Soc. S. Afr. 32, 235 - 246.
- Levy, M.R. (1952) Clues to the past in the Cape flora of today. S. Afr. J. Sci. 49, 155 - 164.
- Levy, M.R. (1954) The genus Muraltia. Jl. S. Afr. Bot. Suppl. Vol. 2.
- Levy, M.R. (1956) Notes on the biology and distribution of the rhenoster bush. S. Afr. J. Sci. 52, 141 - 143.
- Levy, M.R. (1958) The phytogeography of members of the Proteaceae in Africa. Jl. S. Afr. Bot. 24, 1 - 9.
- Levy, M.R. (1964) Migrations and origins of the Cape Flora. Trans. roy. Soc. S. Afr. 37, 85 - 107.
- Levy, M.R. (1970) A revision of the genus Paranomus (Proteaceae). Contrib. Bolus Herb. 2, 1 - 48.
- Linder, H.P. (1982) The historical biogeography of the Disinae (Orchidaceae)
Unpublished Ms.
- Livingstone, D.A. (1975) Late quaternary climatic change in Africa. Ann. Rev. Ecol. Syst. 6, 249 - 280.
- Louw, W.J. (1976) Mesoclimate of the Port Elizabeth-Uitenhage metropolitan area. Pretoria Weather Bureau Technical Paper 4, 1 - 60.
- Martin, A.R.H. (1966) The plant ecology of the Grahamstown Nature Reserve: 2. Some effects of burning. Jl. S. Afr. Bot. 32, 1 - 39.
- Martin, A.R.H. (1968) Pollen analysis of Groenvlei Lake sediments, Knysna. Rev. Palaeobot. Palynol. 7, 107 - 144.
- Martin, A.R.H. & Noel, A.R.A. (1960) The flora of Albany and Bathurst. Rhodes University, Grahamstown.
- Mason, H.L. (1946) The edaphic factor in narrow endemism. II. The geographic occurrence of plants of highly restricted patterns of distribution. Madrono 8, 241 - 257.

- Moll, E.J. & White, F. (1978) The Indian Ocean Coastal Belt. Biogeography and ecology of southern Africa (Ed. by M.J.A. Werger), pp. 561 - 598. Junk, The Hague.
- Nicholson, S.E. & Flohn, H. (1980) African environmental and climatic changes and the general atmospheric circulation in the late Pleistocene and Holocene. Climatic Change 2, 313 - 348.
- Nordenstram, B. (1969) Phytogeography of the genus Euryops (Compositae): a contribution to the phytogeography of southern Africa. Opera botanica 23, 1 - 77.
- Oliver, E.G.H., Linder, H.P. & Rourke, J.P. (1982) Distribution patterns among present-day Cape taxa and their phytogeographical significance. Proceedings of the AETFAT Congress. 18 - 23 Jan., Pretoria.
- Opperman, H. (1978) Excavations in the Buffelskloof rock shelter near Calitzdorp, southern Cape. S. Afr. Archaeol. Bull. 33, 18 - 38.
- Orians, G.H. & Solbrig, O.T. (1977) A cost-income model of leaves and roots with special reference to arid and semi-arid areas. Amer. Natur. 111, 677 - 690.
- Pillans, N.S. (1950) A revision of Agathosma. Jl. S. Afr. Bot. 16, 55 - 183.
- Pillans, N.S. (1954) A revision of Metalasia. Jl. S. Afr. Bot. 20, 47 - 90.
- Raven, P.H. (1964) Catastrophic selection and edaphic endemism. Evolution 18, 336 - 338.
- Reynolds, G.W. (1950) The Aloes of South Africa. The Aloes Book Fund, Cape Town.
- Robson, N.K.B. (1966) Celastraceae. In Flora Zambeziaca. Vol. 2. (Ed. by A.W. Exell, A. Fernandes & H. Wild), pp. 335 - 418. Flora Zambeziaca Managing Committee, London.
- Roberts, B.R., Anderson, E.R. & Fourie, J.H. (1975) Evaluation of natural pastures: quantitative criteria for assessing conditions in the Themeda veld of the Orange Free State. Proc. Grassld. Soc. sth. Afr. 10, 133 - 140.
- Ross, J.H. (1973) An analysis of the flora of Natal. Bothalia 11, 103 - 106.
- Rourke, J.P. (1969) Taxonomic studies on Sorocephalus R. Br. and Spatalla Salisb. Jl. S. Afr. Bot. Suppl. Vol. 7.
- Rourke, J.P. (1972) Taxonomic studies on Leucospermum R. Br. Jl. S. Afr. Bot. Suppl. Vol. 8.
- Ross, J.H. (1973) An analysis of the flora of Natal. Bothalia 11, 103 - 106.

- Schalke, H.J.W.G. (1973.) The upper Quaternary of the Cape Flats area (Cape Province, South Africa). Scripta Geologica 15, 1 - 57.
- Schulze, B.R. (1972) South Africa. In World survey of climatology, vol. 10. Climates of Africa. (Ed. by J.F. Griffiths), pp. 501 - 586. Elsevier, Amsterdam.
- Schulze, R.E. (1975) Incoming radiation on sloping terrain: a general model for use in Southern Africa. Agrochemophysika 7, 55 - 61.
- Schulze, R.E. & McGee, O.S. (1978) Climatic indices and classification in relation to the biogeography of southern Africa. Biogeography and ecology of southern Africa. (Ed. by M.J.A. Werger), pp. 19 - 50. Junk, The Hague.
- Small, E. (1973) Xeromorphy in plants as a possible basis for migration between arid and nutritionally deficient environments. Bot. Not. 126, 534 - 539.
- Specht, R.L. (1979) Heathlands and related shrublands of the world. Heathland and related shrublands of the world. A. Descriptive studies. Ecosystems of the world, vol. 9 (Ed. by R.L. Specht), pp. 1 - 18. Elsevier, Amsterdam.
- Specht, R.L. & Moll, E.J. (1982) Heathlands and sclerophyllous shrublands - an overview. Mediterranean-type ecosystems. The role of nutrients. (Ed. by F.J. Kruger, D.T. Mitchell & J.U.M. Jarvis). Springer Verlag, New York, Berlin & Heidelberg (in press).
- Squires, V.R. & Trollope, W.S.W. (1979) Allelopathy in the karoo shrub, Chrysocoma tenuifolia. S. Afr. J. Sci. 75, 88 - 89.
- Stebbins, G.L. (1974) Flowering plants, evolution above the species level. Edward Arnold, London.
- Stebbins, G.L. & Major J. (1965) Endemism and speciation in the California flora. Ecol. Monogr. 35, 1 - 31.
- Strey, R.G. (1981) Observations on the morphology of the Araliaceae in southern Africa. Journal of Dendrology 1, 66 - 83.
- Strid, A.K. (1972) A revision of the genus Adenandra (Rutaceae). Opera Botanica 32, 1 - 112.
- Takhtajan, A. (1969). Flowering plants: origin and dispersal. Oliver & Boyd, Edinburgh & London.

- Tankard, A.J. & Rogers, J. (1978). Late Cenozoic palaeoenvironments on the west coast of Southern Africa. J. Biogeogr. 5, 319 - 337.
- Taylor, H.C. (1978). Capensis. Biogeography and ecology of southern Africa. (Ed. by M.J.A. Werger), pp. 171 - 229. Junk, The Hague.
- Taylor, H.C. (1980) Phytogeography of fynbos. Bothalia 13, 231 - 235.
- Thoday, D. (1925) The geographical distribution and ecology of Passerina. Ann. Bot. 39, 175 - 208.
- Tinley, K.L. (1975) Habitat physiognomy, structure and relationships. Univ. Pretoria Publ. New Series 97, 67 - 77.
- Tinley, K.L. (1977) Framework of the Gorongosa ecosystem. D. Sc. Thesis, University of Pretoria. Published by the author.
- Tölken, H.R. (1977) A revision of the genus Crassula in southern Africa. Contrib. Bolus Herb. 8, 1 - 595.
- Trollope, W.S.W. (1970) A consideration of macchia (fynbos) encroachment in South Africa and an investigation into methods of macchia eradication in the Amatole Mountains. Unpublished M.Sc. thesis, University of Natal, Pietermaritzburg.
- Van Daalen, J.C. (1980) The colonisation of fynbos and disturbed sites by indigenous forest communities in the southern Cape. Unpublished M.Sc. thesis, University of Cape Town.
- Van Wyk, A.E. & Lötter, L.A. (1982) Manilkaria nicholsonii (Sapotaceae), a new species from Southern Natal. S. Afr. J. Bot. 1, 33 - 37.
- Van Zinderen Bakker, E.M. (1976) The evolution of Late Quaternary palaeoclimates of southern Africa. Palaeoecology of Africa 9, 160 - 202.
- Verdoorn, I.C. (1963) Olea. Flora of southern Africa (Ed. by R.A. Dyer, L.E. Codd and H.B. Rycroft), pp. 112 - 128. Government Printer, Pretoria.
- Vincent, E. (1972) Climatic change at the Pleistocene-Holocene boundary in the southwestern Indian Ocean. Palaeoecology of Africa 6, 45 - 54.
- Vogel, J.C. (1978) Isotopic assessment of the dietary habits of ungulates. S. Afr. J. Sci. 74, 298 - 301.
- Vuilleumier, F. & Simberloff, D. (1980) Ecology versus history as determinants of patchy and insular distribution in high Andean birds. Evolutionary Biology 13, 235 - 379.

- Weather Bureau (1954) Climate of South Africa. Part 2. Rainfall statistics.
Weather Bureau, Pretoria (WB 20).
- Weimarck, H. (1941) Phytogeographical groups, centres and intervals within the Cape Flora. Lunds Universiteits Arsskrif. N.F. Adv. Z Bd. 37, 1 - 143.
- Wellington, J.H. (1955) Southern Africa. A geographical study. Vol. 1.
Cambridge University Press, Cambridge.
- Werger, M.J.A. (1978a) The Karoo-Namib Region. Biogeography and ecology of southern Africa. (Ed. by M.J.A. Werger), pp. 233 - 299,
Junk, The Hague.
- Werger, M.J.A. (1978b) Biogeographical division of Southern Africa. Biogeography and ecology of southern Africa. (Ed. by M.J.A. Werger),
pp. 147 - 170. Junk, The Hague.
- Werger, M.J.A. & Coetzee, B.J. (1978) The Sudano-Zambezian Region. Biogeography and ecology of southern Africa. (Ed. by M.J.A. Werger),
pp. 301 - 462. Junk, The Hague.
- White, A., Dyer, R.A. & Sloane, B.L. (1941) The succulent Euphorbieae of southern Africa, vols. 1 & 2. Abbey Garden Press, Pasadena, California.
- White, F. (1962) Geographic variation and speciation in Africa with particular reference to Diospyros. Syst. Ass. Publ. 4, 71 - 103.
- White, F. (1971) The taxonomic and ecological basis of chorology. Mitt. Bot. Staatssamml. Munchen 10, 91 - 112.
- White, F. (1976a) The vegetation map of Africa. The history of a completed project. Boissiera 24, 659 - 666.
- White, F. (1976b) The underground forests of Africa: a preliminary review. Gard. Bull. Singapore 29, 57 - 71.
- White, F. (1978) The Afromontane Region. Biogeography and ecology of southern Africa. (Ed. by M.J.A. Werger), pp. 465 - 510. Junk, The Hague.
- White, F. (ed.) (1982) Vegetation of Africa. UNESCO, Paris (in press).
- Wild, H. (1964) The endemic species of the Chimanimani Mountains and their significance. Kirkia 4, 125 - 157.
- Wild, H. (1968) Phytogeography of South Central Africa. Kirkia 6, 197 - 222.
- Williams, I.J.M. (1972) A revision of the genus Leucadendron. Contrib. Bolus Herb. 3, 1 - 425.

PAPER 3

DIVERSITY RELATIONS IN CAPE SHRUBLANDS AND OTHER VEGETATION IN
THE SOUTH EASTERN CAPE, SOUTH AFRICA

Abstract

This paper investigates, and seeks explanations for, the diversity relations of Cape shrublands (fynbos and renosterveld), subtropical thicket and Afromontane forest, in the biogeographically complex S.E. Cape. Global comparisons of richness at the tenth hectare scale, of communities in the study area and elsewhere in South Africa with analogous vegetation on other continents, were largely inconclusive. Reasons for this are the unexplained variability of richness within vegetation types, problems associated with the scale of diversity used, and difficulties in defining analogous vegetation types. Diversity comparisons within the Cape Region and within the study area communities showed that alpha diversity of fynbos was not consistently higher than other vegetation types. In the study area highest richness was recorded in renosterveld and highest equitability in subtropical thicket; the most species-poor communities were Mountain Fynbos and Afromontane forest. The results of a correlation analysis showed that an index of phytochorological diversity was the factor most strongly correlated with richness in all vegetation types. Soil nutrients did not emerge as significant correlates of diversity except in fynbos where low levels of available nutrients were associated with low values of phytochorological diversity and low species richness. The diversity of fire-prone and grazed communities could be partly explained by non-equilibrium models of species diversity. Ecological and historical hypotheses were presented as explanations for the richness of communities having island-like distributions in the study area. It was generally concluded that historical and ecological factors should be given equal weight in descriptive studies which seek regional and global explanations of the evolution and maintenance of species diversity.

<u>Contents</u>	Page
Introduction	208
Study area	209
Geology, physiography and climate	209
Vegetation and soils	210
Methods	211
Data collection	211
Data analysis	212
Results	215
Global comparisons at the tenth-hectare scale	215
Diversity patterns in the study area	219
Alpha diversity	219
Beta diversity	221
Correlation analysis	222
Dynamics and disturbance	229
Discussion	235
Global comparisons	235
Diversity patterns in the study area: Cape comparisons	236
Phytochorological complexity and tension zones	237
Equilibrium biogeography versus history	238
Dynamics and disturbance	241
The role of soil nutrients	242
Other hypotheses	243
Concluding remarks	244
References	245

Introduction

Species diversity is a perennial topic in biology which has long intrigued theoreticians and empiricists alike. An understanding of the factors which regulate diversity is central to the science of conservation. However there appears to be no theory of plant species diversity which is consistently corroborated by data from varied communities on different parts of the globe. Even within the relatively well circumscribed and intensively studied North American temperate forests, the prediction of species diversity remains elusive (Glenn Lewin, 1977; Peet, 1978).

Cape fynbos vegetation has acquired a reputation for high diversity at all levels (Taylor, 1978; Kruger, 1979) although few data have been published. Campbell and Van der Muelen⁽¹⁹⁸⁰⁾ have investigated patterns of alpha and beta diversity along a successional gradient in south western (S.W.) Cape fynbos. Kruger and Taylor (1979) have demonstrated spectacularly high levels of gamma and delta diversity in the Mountain Fynbos of the S.W. Cape. It is not known whether these patterns are generalizable for the remainder of the Fynbos Biome (sensu Kruger, 1978). There are no published data dealing with diversity relations of the fynbos communities in the southern and south eastern regions of the Fynbos Biome.

This paper reports on, and contrasts patterns of species diversity in Cape shrublands (fynbos and renosterveld), subtropical thicket and Afromontane forest in the south eastern (S.E.) Cape at the eastern boundary of the Fynbos Biome. The aim of the study was to generate hypotheses to explain the evolution and maintenance of diversity in the communities studied. Due to our poor understanding of continental plant species diversity relations, there is no general deductive model from which test implications can be deduced. The usual approach is to use descriptive techniques such as correlation analysis to explore diversity patterns and derive inductive predictions of diversity based on the available data (Glenn Lewin, 1977).

In the first part of this paper I present data from the study area and elsewhere in South Africa on species diversity and growth form richness at the tenth hectare scale. I discuss global comparisons of richness at this scale for analogous vegetation types. Next I explore diversity relations within the study area communities. Correlation analysis was used to isolate those factors which show strong relationships with measures of diversity. Independent variables used in the analysis included topographic, climatic, soil and disturbance factors as well as an index which reflected the degree of intermingling of floras from different phytochoria.

The results of the study are discussed in terms of current theories of plant species diversity and new hypotheses are presented. Phytochorological diversity emerged as the factor showing significant correlations with species richness in both Cape shrublands and the non-Cape communities. I found considerable support for non-equilibrium hypotheses (Connel, 1978; Huston, 1979) in explaining the diversity relations of fire-prone Cape shrublands. The relative roles of history and ecology were contrasted in explaining the diversity patterns of communities having an insular distribution in the study area.

Study area

The study area is located in the Humansdorp (34°02'S, 24°47'E) region of the S.E. Cape. Details of the environment and vegetation of the study area are given elsewhere (Cowling, 1982a); below I present only those features which are directly relevant to this paper.

Physiography, geology and climate

Most of the region comprises a coastal plain (0 - 300m) which cuts across sandstones and quartzites of the Table Mountain Group, shales of the Bokkeveld Group, and conglomerates of the Uitenhage Group. Along the coast there are recent deposits of calcareous dune sands and calcrete. An important feature in the eastern part of the area is the deep and wide alluvial valley of the Gamtoos River which is incised into the rocks of the Uitenhage Group. The south western wall of the valley is composed of conglomerates while the lower western wall comprises soft sandstones and mudstones with coarse-grained sandstones and conglomerates higher up. Above these last-mentioned Uitenhage deposits is a faulted block of limestones and phyllites of the Malmesbury Supergroup. Resting on these are quartzites of the Table Mountain Group which comprise the Elandsberg Range (700 - 1 000 m), an east trending axis of the Cape Folded Belt which towers above the Gamtoos Valley.

The climate is warm temperate and transitional between Köppen Csb and Cfb climates (Schulze & McGee, 1978). I recognized three climatic types in the study area (Cowling, 1982a).

(i) Coastal plain subhumid climate.

The climate is mild with low diurnal and annual temperature ranges. The average annual temperature at Cape St. Francis on the coast is 17.0°C and the average annual rainfall is 666 mm. The rainfall at Humansdorp, also on the coastal plain, is 667 mm. Rain can fall at any time of the year but the summer

months (Dec., Jan. and Feb.) are always driest.

(ii) Semi-arid valley climate

The river valleys of the S.E. Cape have a warmer, drier and more variable climate than the adjacent mountains and interfluves : temperature extremes are great and rainfall variability is high (Anon., 1942; Louw, 1976). At Uitenhage in the nearby Swartkops valley the average annual temperature is 18.1°C and at Hankey, in the Gamtoos valley, the average annual rainfall is 432 mm. Rainfall distribution is bimodal with spring and autumn peaks.

(iii) Humid coastal mountain climate

In the S.E. Cape, where rainfall is under strong orographic control, the highest precipitation is recorded on the coastal axis of the Cape Folded Belt. In the study area the upper seaward slopes of the Elandsberg range receive more than $1\,000\text{ mm yr}^{-1}$. Rainfall peaks are in autumn and spring. Temperatures are equable but lower than the surrounding lowlands and light frosts and snow are occasionally recorded in winter. I consider this climate most favourable for plant growth, or mesic, in a universal sense (Peet, 1978).

Vegetation and soils

The vegetation of the study area has been classified hierarchically into a series of classes, orders and communities (Cowling, 1982a; see Table 3 for syntaxonomic hierarchy and nomenclature). Below, I explain briefly my class and order concepts and describe the major soil-vegetation relationships. Detailed soil data are given in Cowling (1982a).

The class Cape Fynbos Shrublands comprises the shrublands and heathlands of the Cape Floristic Region which are confined to acid infertile sands and alkaline calcareous sands (see Taylor, 1978; Kruger, 1979 for reviews). I recognized three orders in the study area. S.E. Mountain Fynbos is a chorologically pure fynbos confined to upper moist slopes of the Elandsberg and other ranges in the S.E. Cape. Soils are extremely acid and highly infertile loamy sands. Grassy Fynbos is a chorologically complex fynbos type which occurs on the north and lower slopes, and planed surfaces of the Cape Folded Belt in the S.E. Cape. It occupies drier, warmer and more fertile sites than the Mountain Fynbos. Grassy Fynbos has a high cover of subtropical C_4 grasses which largely replace Restionaceae. South Coast Dune Fynbos is restricted to calcareous dune sands along the southern (S) and S.E. Cape coasts. It differs from other fynbos types in lacking Proteaceae and having a strong subtropical thicket shrub component.

The class Cape Transitional Small-leaved Shrublands comprise the non-fynbos small-leaved shrublands of the Cape Region and occur on the fine-grained and moderately fertile soils of the coastal forelands and intermontane valleys. Although many of the constituent species are confined to Cape Region, most are chorological transgressors. I recognized one order in the study area - South Coast Renosterveld. This shrubland type is restricted to the S. and S.E. Cape coastal forelands. The dominant shrub is Elytropappus rhinocerotis. Grasses and geophytes are conspicuous in the understorey. Much of the South Coast Renosterveld has been derived from grassland in historical times (Cowling, 1982a).

A non-Cape class of shrublands is the Subtropical Transitional Thicket. Structurally these thickets are best described as a tangle of evergreen, spiny, sclerophyllous shrubs and vines with a high cover of succulents in drier regions. Typical tropical-subtropical shrub and tree genera are Euclea, Diospyros, Sideroxylon, Rhus and Cassine and karroid succulent genera include Crassula, Euphorbia, Delosperma and Zygophyllum. In the Cape, subtropical thicket is confined to deep, well-drained fertile soils of the coastal forelands and intermontane valleys. I recognized two orders in the study area. Kaffrarian Thicket is a non-succulent type with fairly strong Afromontane affinities. Kaffrarian Succulent Thicket is confined to the hot, dry river valleys of the S. and S.E. Cape. It is characterized by a strong incidence of succulents including many species of karroid affinity. Unlike the fynbos and renosterveld communities, thickets are not fire-prone and, in the study area, are ungrazed.

Afromontane Forest is a class of temperate African mountain forests distributed in an archipelago of mountain "islands" from Somalia to the Cape Peninsula (White, 1978).

Character taxa include Podocarpus spp., Ocotea bullata, Rapanea melanophloeas, and Curtisia dentata. In the study area this forest type is confined to small patches on deep, colluvial soils in the Elandsberg Mountains.

Methods

Data collection

I sampled a total of 194 plots selectively located in the study area to cover the fullest possible range of vegetational diversity and disturbance regimes. It was necessary to standardize plot size since a comparison of species richness requires equal plot sizes.

I therefore established an optimal plot size for all vegetation types which would give a compromise between effort expended and information obtained. 19 standard 1 - 1 000 m² samples

(Naveh & Whittaker, 1979; Whittaker *et al.*, 1979) were located in a wide range of vegetation types in the study area (Table 2). Using the species-area relationship and regarding one hectare as having an information content of 100% (Werger, 1972), I was able to determine the information content for plot sizes of 1, 5, 10, 100 and 1 000 m². 100 m² plots gave an information content ranging from 39% to 64% with a mean and standard deviation of 55.1% \pm 7.5% for all vegetation types including grasslands, shrublands and forests. The information content of 14 of the 19 samples fell within the range of 55% - 65%. The two samples falling well below this range (38.8% and 42.6%) were on coastal dunes where a complex successional mosaic made it difficult to select homogeneous 0.1 ha stands. I used 10m x 10m plots in all vegetation types of the study area. The tenth-hectare plots sampled in the study area and elsewhere in South Africa (Table 2), provided the data for global comparisons of species richness at this scale (cf. Naveh & Whittaker, 1979; Rice and Westoby, 1982a).

In each 100m² plot I subjectively estimated the projected canopy cover of each species and recorded a range of site variables including aspects of community structure, site topography, climate, soil and biotic factors including post-disturbance vegetation age and grazing intensity. Table 1 lists these variables with some information on classes and methods.

Data analysis

Alpha diversity

Alpha diversity is defined as the within-habitat or intra-community diversity (Whittaker, 1960; 1972) and is the major focus of this paper. Species richness (\underline{S}) is an unambiguous, biologically appropriate measure (Peet, 1974; Whittaker, 1972; 1977) defined simply as the number of species per site. Heterogeneity or mixed-diversity measures incorporate both the concepts of species richness and species evenness (Peet, 1974). I used Simpson's index (\underline{C}) which expresses the relative concentration of dominance by measuring the probability that two individuals selected at random from a sample will belong to the same species; and the Shannon-Wiener function ($\underline{H'}$), an equitability index which measures the apportionment of individuals or cover among species (Whittaker, 1972; Peet, 1974). Where it was necessary to show graphical comparisons of these indices, the reciprocal of \underline{C} and the exponential form of $\underline{H'}$ were used (Hill, 1973a). Percentage canopy cover was used to give importance values for species.

Table 1. Environmental and biotic variables recorded in plots and used as independent variables in the correlation analyses. Soil chemical data from the A horizon only and for a subset of 97 plots. Some details on classes of variables and methods are shown. Abbreviations are those used in Tables 4 - 7.

Variable	Abbreviation	Classes of variables and methods
Vegetation age (yr)	VAG	Post-fire, post-bush cut. Estimates based on information from landowners
Grazing intensity	GRZ	Classes: ungrazed = 1, light = 2, moderate = 3, heavy = 4, overgrazed = 5. Scale based on current stocking rate, past grazing and the effects of grazing (cf. Roberts <i>et al.</i> , 1975)
Annual rainfall (mmyr ⁻¹)	RAI	Data from 1:250,000 isohyet maps and local weather stations
Altitude (m)	ALT	From 1:50,000 topographic sheets
Aspect	ASP	Classes: 1 = SE, 2 = S, 3 = SW, 4 = E, 5 = W, 6 = NE, 7 = N, 8 = NW: a cool to hot gradient estimated from aspect-radiation flux data (Schulze, 1975)
Slope inclination	SLO	Slope angle in degrees
Litter cover (%)	LIT	Subjective estimate
Rock cover (%)	RCO	Subjective estimate
Soil depth (m)	SDE	Estimated from augerings in each plot or, for stony soils, from roadside cuttings and other disturbances
Sand content (%)	SAN	Estimated by feel for all plots and tested using the results of a textural analysis (pipette method) of samples from 97 plots
Soil pH	PHH	1 N KCl 1 : 2.5 soln.
Exchangeable calcium (ppm)	CAC)	1 NH ₄ acetate leachate
S-value (sum of exchangeable bases) (meq %)	BAS)	
Oxidizable carbon (%)	CAR	Walkley-Black method
Total nitrogen (%)	NIT	Kjeldahl
Available phosphorus (ppm)	PHO	Bray No. 2 (acid extraction, pH 3) Modified Olsen (alkali extraction, pH 8)

Values of species numbers and area for the tenth-hectare samples were fitted by the semi-log form of the least squares regression $\underline{S} = \underline{b} + \underline{d} \log \underline{A}$ in which \underline{S} is species number, \underline{A} is area in m^2 . The coefficients \underline{b} (mean number of plant species in a 1-m^2 plot) and \underline{d} (rate of increase in species numbers with increasing plot area) are then diversity expressions that may be compared with \underline{S} for $1\,000\text{ m}^2$ (Naveh & Whittaker, 1979; Whittaker *et al.*, 1979).

Beta diversity

Beta diversity is between-habitat diversity defined as the changes in species composition along environmental gradients and is measured in terms of half-changes (HC) (Whittaker, 1960). I estimated the beta diversity along parallel coenoclines (Whittaker, 1973) in fynbos and non-fynbos (thicket, forest) communities. The coenoclines spanned a 500 m elevational range in the Gamtoos Valley and Elandsberg Mountains (Cowling & Campbell, 1982). At approximately 100m intervals four 100 m^2 plots were placed on each aspect on uniformly moderate slopes at corresponding stations along the fynbos and non-fynbos coenoclines, thus facilitating beta diversity comparisons. Beta diversity was expressed in half-changes and calculated from the first reciprocal averaging (RA; Hill, 1973b) eigenvalue (EV) from ordinations of both coenoclines, by the relationship

$$\text{HC} = \sqrt{12\text{EV} / (1 - \text{EV})} / 1.349$$

(Whittaker *et al.*, 1979; see also Olsvig, 1979). This method slightly overestimates beta diversity when compared to Whittaker's (1960) graphical method (Olsvig, 1979; Whittaker *et al.*, 1979).

Phytochorological diversity (PD)

I determined the phytochorological affinities of each species in terms of established phytochoria (Werger, 1978) and computed an index of phytochorological diversity (referred to as PD in Tables 4 - 7) for all plots. The distribution of taxa were established from locality records in the Albany Museum Herbarium (GRA) and the Bolus Herbarium (BOL) and also from relevant taxonomic revisions. Species were classified as:

- (i) endemic to a particular phytochorion;
- (ii) linking two (usually) adjacent phytochoria;
- (iii) widely distributed, common in tropical and subtropical phytochoria;
- (iv) widely distributed, occurring in temperate and tropical phytochoria and often having extra-African distributions.

Categories (ii) – (iv) are ecological and chorological transgressor species (White, 1978). Details on the distribution tracks and examples of species distributions are given in Cowling (1982b). A list showing the classification of species into the phytochorological groups is available on request.

I used the Shannon–Wiener index to compute phytochorological diversity where

$$PD = - \sum p_i \log p_i$$

in which p_i is the number of species in phytochorological group i expressed as a fraction of the total number of species in the plot.

Correlation analysis

I used simple and stepwise multiple correlation analysis computed by forward selection (Draper & Smith, 1966) using the factors shown in Table 1 and PD as independent variables against each of the diversity variables. The stepwise algorithm selectively entered independent variables only if they made a significant contribution at the .10 level. All variables entered were untransformed.

Because the fynbos-renosterveld and forest-thicket communities are fundamentally different in their biogeographical affinities (Cowling, 1982b), structure, and disturbance régimes (Cowling, 1982a), these data sets were analysed separately, in addition to an analysis of the full data set. Only those plots with the full complement of measured soil variables were used in the correlation analysis, thus reducing the sample to 97 plots.

Results

Global comparisons at the tenth-hectare scale

Recent years have seen expanding knowledge on alpha richness at the tenth hectare scale from different vegetation types throughout the world. Comparisons of richness have led to the formulation of theories to explain global similarities and differences in analogous vegetation types (Whittaker, 1977; Naveh & Whittaker, 1979; Rice & Westoby, 1982a). Table 2 shows species diversity and growth form richness at the tenth-hectare scale from 19 sites in the study area and 11 sites elsewhere in South Africa. The data are depicted in a way that makes them directly comparable to other published sources (e.g. Naveh & Whittaker, 1979).

The Cape Fynbos Shrublands in the study area (samples 1 - 9) showed variable richness with a mean of 66.4 species and a range of 41 - 93. Most of the species are shrubs and perennial herbs, particularly graminoids; geophytes are common but annuals are rare. This growth form spectrum seems typical of southern hemisphere heathlands on infertile soils (Kruger, 1979; Naveh & Whittaker, 1979; Specht, 1979; Rice & Westoby, 1982b). Dominance concentration (\underline{C}) was generally low and equitability ($\underline{H'}$) high for all samples (cf. Westman, 1982). Kruger (1979) gives a mean of 65.0 and a range of 31 - 126 species per 0.1 ha for eight fynbos samples from the S.W. Cape, and Naveh & Whittaker (1979) report a mean of 75.0 and a range of 52 - 128 species from 10 S.W. Cape fynbos samples.

In common with Cape fynbos, Australian heathlands are also reputed to have high alpha diversity (Marchant, 1973; Lamont *et al.*, 1977; Whittaker, 1977; George *et al.*, 1979; Naveh & Whittaker, 1979; Rice & Westoby, 1982a; b; Hnatiuk & Hopkins, 1981).

Naveh & Whittaker (1979) report a mean of 65.0 with a range of 46 - 82 species, and a mean value of \underline{C} of 0.22, from seven Western Australian kwongan (heath) samples.

George *et al.* (1979) give species-area data for kwongan which show that at the tenth-hectare scale, eight samples had a mean of 60.6 and a range of 49 - 81 species.

Hnatiuk & Hopkins (1981) report species numbers per 0.1 ha of 46.3 ± 18.3 ($\underline{n} = 11$), 82.3 ± 16.1 ($\underline{n} = 42$) and 91.1 ± 13.6 ($\underline{n} = 32$) from three kwongan communities on a relatively dry (550 mm yr^{-1}) lateritic plateau in Western Australia. Rice and Westoby (1982b) present data for standard tenth-hectare samples from woodlands ($\bar{X} = 77.9 \pm 9$; $\underline{n} = 12$), wet scrub ($\bar{X} = 48.8 \pm 8$; $\underline{n} = 2$), and dry scrub ($\bar{X} = 56 \pm 7$; $\underline{n} = 12$) on infertile sandstone-derived soils near Sydney. All communities had strong heathland (*sensu* Specht, 1979) characteristics.

Samples 10 - 18 in Table 2 are Cape Transitional Small-leaved Shrublands. All samples belong to the Coast Renosterveld (Acocks, 1953; Taylor, 1978; Boucher & Moll, 1980) and while samples 10 - 14 are confined to the study area, the remaining samples span the full range of this vegetation type from the winter rainfall region of the S.W. Cape to the transitional summer rainfall region of the S.E. Cape. These communities occur on moderately fertile loams to clay-loams and are therefore somewhat comparable to mediterranean-type shrublands (*sensu* Di Castri, 1980). In the renosterveld samples richness was higher than all fynbos and most kwongan data presented above, with a mean of 83.8 and a range of 57 - 103 species; values of \underline{C} and $\underline{H'}$ were higher and lower respectively than the fynbos data shown in Table 2. Of particular interest in the renosterveld communities is the exceptional wealth of geophytes.

Renosterveld appears to be more diverse than its putative analogues in other mediterranean-type regions including the mesic, evergreen, sclerophyllous types (e.g. maqui, chaparral, mallee; Naveh & Whittaker, 1979) and the xeric, drought-deciduous, mesophyllous types (e.g. coastal sage scrub, phrygana; Westman, 1981). However it is poorer than grazed open shrublands and woodlands of Israel where Naveh & Whittaker (1979) found up to 197 species per 0.1 ha in disturbed, annual-rich communities.

Table 2 shows a succulent karroid shrubland (Acocks, 1953) sample on fertile clay-loam in a xerothermic mediterranean climate (average rainfall of 213 mm yr^{-1}) in the S.W. Cape. Overall richness is low but there is a high diversity of succulent sub-shrubs. Werger (1972) gives species-area data for nine non-succulent karroid communities from the semi-arid regions of the northern Cape; he recorded a mean of 46.8 species per 0.12 ha with a range of 25 - 61. Rice & Westoby (1982a) report a mean of 64.7 species from semi-arid chenopod shrublands in New South Wales where soils are red clay-loams and rainfall is non-seasonal 200 mm yr^{-1} . About 60% of the species in the Australian shrublands are annuals. Due to the time of sampling the full complement of annuals and geophytes were not recorded at the South African karoo site. Whittaker & Niering (1965, 1968) record a range of 57 - 70 species in Sonoran Desert scrub and desert grassland on limestone in the semi-arid, near subtropical climate of the lower slopes of the Santa Catalina Mountains in Arizona. These figures include both summer and winter annuals.

Samples from subtropical thicket are mostly from the study area (20 - 24) but include a dune thicket sample from elsewhere in the S.E. Cape (25) and from the S.W. Cape (26) (Table 2). These thickets, especially the drier ones, have a wealth of growth forms including large-leaved sclerophyll trees, shrubs and vines, arborescent stem and leaf succulents, succulent shrubs and vines, forbs, graminoids and geophytes. Subtropical thicket is moderately rich with the highest species numbers recorded in the dry succulent types (samples 23 and 24) and lowest numbers in the dune thickets (samples 22, 25 and 26) especially the depauperate sample from the S.W. Cape. Equitability is higher than fynbos samples. These thickets are a subtropical formation which have recently penetrated into the temperate Cape (Cowling, 1982b) and have no clear analogue in other mediterranean and sub-mediterranean regions. Boucher and Moll (1980) and Specht & Moll (1982) call the south western Cape thickets mediterranean shrublands (*sensu* Di Castri, 1980), a clearly erroneous interpretation since affinities are strongly tropical and there are very few species endemic to the Cape mediterranean-climate region (Cowling, 1982b). Samples 23 and 24

Table 3. Alpha diversities in 100m² plots in communities of the study area, expressed as species richness (S) and heterogeneity-diversity (H' = Shannon-Wiener index, C = Simpsons index). Also shown is the total number of species recorded in combined samples from each community.

Syntaxa ¹	n^2	n^3	S			H'			C			Total species numbers in combined samples
			\bar{X}	SD	range	\bar{X}	SD	range	\bar{X}	SD	range	
CAPE FYNBOS SHRUBLANDS												
S.E. Mountain Fynbos												
<u>Tetradlea-Thamnos</u> community	8	4	26.4	5.3	22-36	1.03	.13	.83-1.22	.13	.05	.08-.22	87
<u>Leucospermum-Tetradlea</u>	5	2	26.6	4.6	22-34	1.00	.07	.90-1.10	.14	.02	.13-.18	56
Grassy Fynbos												
<u>Thamnoschortus-Erica</u>	5	3	33.8	9.2	24-45	1.10	.14	.93-1.27	.14	.05	.07-.20	69
<u>Protea-Clusia</u>	9	4	43.5	9.8	35-66	1.09	.13	.85-1.30	.13	.04	.09-.21	128
<u>Erica-Trachypogon</u>	16	9	40.1	8.4	28-56	1.08	.17	.56-1.30	.14	.10	.08-.51	212
<u>Themeda-Passerina</u>	4	2	36.3	4.5	30-40	1.00	.15	.82-1.20	.17	.06	.09-.24	92
<u>Thamnoschortus-Tristachya</u>	7	5	46.6	4.7	38-51	1.20	.04	1.16-1.27	.10	.02	.07-.13	133
South Coast Dune Fynbos												
<u>Restio-Agathosma</u>	13	6	32.4	11.2	14-58	.97	.18	.54-1.16	.17	.10	.11-.48	144
<u>Restio-Maytenus</u>	12	4	33.5	8.4	25-51	1.04	.19	.83-1.36	.17	.09	.06-.35	114
<u>Themeda-Stenotaphrum</u>	5	3	40.2	5.0	32-45	.81	.07	.72-.89	.27	.04	.25-.34	104
CAPE TRANSITIONAL SMALL-LEAVED SHRUBLANDS												
South Coast Renosterveld												
<u>Themeda-Cliffortia</u>	11	6	33.6	8.4	21-48	.72	.24	.44-1.17	.39	.17	.09-.65	120
<u>Elytropappus-Eustachys</u>	10	5	51.5	14.7	36-73	1.11	.19	.87-1.34	.19	.13	.07-.51	162
<u>Elytropappus-Metastasia</u>	12	7	40.8	7.8	26-52	.94	.19	.69-1.34	.23	.11	.07-.46	152
<u>Elytropappus-Relbunium</u>	4	1	42.5	11.9	35-60	.81	.28	.53-1.17	.36	.21	.11-.57	97
AFROMONTANE FOREST												
Knysna Afromontane Forest												
<u>Rapanea-Canthium</u>	5	2	32.8	2.3	30-36	1.12	.12	.90-1.21	.12	.07	.09-.24	71
<u>Rapanea-Ocotea</u>	4	2	21.2	2.1	19-24	.97	.07	.87-1.04	.16	.04	.12-.21	34
SUBTROPICAL TRANSITIONAL THICKET												
Kaffrarian Thicket												
<u>Pterocelastrus-Gonioma</u>	11	4	36.9	7.8	23-46	1.24	.13	1.02-1.39	.08	.03	.06-.14	107
<u>Pterocelastrus-Euclea</u>	18	8	37.3	8.1	26-54	1.19	.19	.80-1.44	.11	.07	.04-.33	130
<u>Cassine-Cussonia</u>	12	5	24.6	6.1	13-37	.92	.20	.61-1.21	.21	.09	.11-.39	93
<u>Cassine-Schotia</u>	5	2	29.6	7.2	21-37	1.14	.13	1.01-1.31	.12	.04	.06-.15	67
Kaffrarian Succulent Thicket												
<u>Sideroxylon-Euphorbia</u>	15	7	35.8	10.9	20-52	1.21	.10	1.01-1.37	.09	.02	.06-.12	120
<u>Euclea-Brachylaena</u>	5	3	45.0	7.6	39-56	1.26	.08	1.16-1.35	.09	.02	.07-.11	108

¹ Hierarchy of classes, orders and communities (Cowling, 1982a).

² Total number of samples used to compute diversity indices.

³ Samples with soil data used in correlation analyses.

have similar climatic and soil conditions to the Australian mallee community studied by Whittaker *et al.* (1979) who recorded a mean of 52.7 and a range of 49 – 62 species in 10 0.1 ha samples. However unlike the South African thicket, the mallee community is a fire-prone, open shrubland with few vines and succulents, and numerous annuals.

The two forest samples in Table 2 include a subtropical coastal forest (Acocks, 1953) from Natal (sample 27) and a temperate Afromontane forest from the study area (sample 30). Rice & Westoby (1982a) quote data on the richness of Australian tropical rainforests which are considerably more diverse than the Natal forest sample. There is a large body of data on species richness in 0.1 ha plots from North American temperate forests (see Whittaker, 1969, 1972, 1977 for reviews; Peet, 1978), where species numbers average about 50 but values as low as 4 and as high as 115 have been recorded (Westoby & Rice, 1982a). Whittaker gives a mean of 47.7 and a range of 29 – 105 species from 28 0.1 ha samples of temperate Australian forests and woodlands. Rice & Westoby (1982a) noted similar richness values for their Australian temperate forest samples and the North American forests. The richness of the single sample from the study area falls within the range of the Australian and North American forests.

The two remaining samples are from species-rich coastal subtropical grassland and savanna on acid, sandy, infertile lithosols derived from T.M.G. sandstones. The communities are dominated by tropical C₄ grasses but include species of typical Cape fynbos genera (e.g. *Protea*, *Agathosma*, *Watsonia*, *Aristea*). The geophytic flora is relatively rich. Very few data are available from analogous communities on other continents. Cerrado, a tropical Brazilian savanna confined to infertile sands is well noted for its floristic richness where about 230 species were reported in 0.1 ha (Eiten, 1978). Rice & Westoby (1981a) give a range of 25 – 50 species in north Australian tropical grassy woodlands.

Diversity patterns in the study area

Alpha diversity

Table 3 shows patterns of alpha diversity in 100 m² plots from communities in the study area. Within the Cape shrublands, S.E. Mountain Fynbos had the lowest richness (S) but values of dominance concentration (C) and equitability (H') were comparable to other fynbos communities. Mountain Fynbos was poorer than all forest and thicket except for the *Rapanea-Ocotea* Afromontane forest community. A comparison with

richness data from S. and S.W. Cape Mountain Fynbos communities stresses the depauperate nature of the S.E. Mountain Fynbos. Mean number of species recorded in 50 m² samples from three Mountain Fynbos communities at Jonkershoek, S.W. Cape, were 39, 39 and 50 (Werger *et al.*, 1972). Mean species numbers recorded in 124 50 m² Mountain Fynbos samples (excluding azonal communities) from Cape Hangklip, S.W. Cape, was 32.2 ± 8.9 (Boucher, 1978). More precisely comparable data come from Bond's (1981) study in the southern Cape mountains. In the Outeniqua Mountains, some 260 km west of the study area, he recognized Mesic Proteoid Shrublands which share with the S.E. Mountain Fynbos, similar climate, soils and dominant proteoid and graminoid species. In three communities comparable to those in the study area, Bond (1981) recorded mean species richness in 50 m² samples of 30.2 (range = 21 - 37), 41.8 (35 - 48) and 33.2 (29 - 39).

Grassy Fynbos communities showed variable values of S, H' and C (Table 3). The least diverse community (Thamnochortus-Erica) had the lowest values of phytochorological diversity (PD) and the poorest soils; the most diverse community (Thamnochortus-Tristachya) is a restioid grassland (*sensu* Campbell *et al.*, 1981) which is frequently burnt or mowed and moderately grazed by domestic livestock.

Dune Fynbos communities were poorer than Grassy Fynbos and had lower and higher values of H' and C respectively. Highest richness but lowest equitability were recorded for the Themeda-Stenotaphrum community which is mowed and grazed. Van der Merwe (1976) reported a richness per 100 m² plots of 30.9 (16 - 42) and 33.3 (11 - 54) in two Dune Fynbos communities 200 km west of the study area.

In the study area S was generally highest in the renosterveld communities but C was consistently high reflecting the greater dominance by one or few species. Lowest diversity was in the most mesic community (Themeda-Cliffortia) on seasonally water-logged soils while highest diversity was in the drier Elytropappus-Eustachys community on well-drained, sandy, stony soils.

Within the forest and thicket communities, Afromontane forest was least diverse. The drier Rapanea-Canthium community with its strong admixture of subtropical forest trees and vines was richer than the cooler, wetter and chorologically purer Rapanea-Ocotea community. Data from Campbell & Moll (1977) and McKenzie *et al.* (1977) indicate a mean of about 18 species in 100 m² plots from chorologically pure Afromontane

forests on the Cape Peninsula. McKenzie's (1978) data for S.W. Cape Afromontane forests show a mean of about 19 species in 100 m² plots. However there is a distinct tendency for alpha richness to increase in forest patches closest to the Knysna forest "source area" (cf. Cody, 1982).

Diversity, particularly heterogeneity diversity, was highest in the dry succulent thickets and lowest in the dune thickets (Cassine-Cussonia, Cassine-Schotia). Van der Merwe (1976) recorded a similar richness in 100 m² samples (\bar{X} : 24.7; range : 16 - 41) for a community almost identical to the Cassine-Cussonia community in Table 3. In related communities on calcareous substrates in the S.W. Cape, Van der Merwe (1977) recorded mean species richness of 11.3 (6 - 22) and 19.9 (6 - 32) in 100 m² samples. These data further illustrate the westwards depauperization of subtropical thicket in the Cape Region (Cowling, 1982b).

Community richness, expressed as the total number of species in combined samples (Table 3) showed interesting patterns which did not always correlate with sample means. Comparing communities with similar sample sizes, it can be inferred that highest community richness was recorded in Grassy Fynbos and renosterveld communities. Thicket communities with similar means for \bar{S} had a lower overall community richness which could mean a lower beta diversity.

Beta diversity

The fynbos coenocline (FC) included S. Coast Renosterveld and Grassy Fynbos at the two lower stations and S.E. Mountain Fynbos for the rest of the transect. The non-fynbos coenoclines (N-FC) spanned a gradient ranging from succulent thicket at the two lowest stations, through non-succulent thicket at station 3, and then to Afromontane forest at the two uppermost stations (for details see Cowling & Campbell, 1982). The first axis of the RA ordinations of both coenoclines arranged the samples in a sequence which was faithful representation of the stations along the elevational gradient. Both coenoclines are arranged along strong gradients of increasing altitude and rainfall and weaker gradients of decreasing soil pH and exchangeable bases (Cowling & Campbell, 1982). All stations along the N-FC had deeper, heavier and more fertile soils than corresponding FC stations.

I computed 5.48 HC (1 HC = 76.6 m) for the FC and 8.95 HC (1 HC = 46.9 m) for the N-FC along the parallel gradients. When compared to data collected elsewhere, these values represent very high levels of species turnover. Whittaker (1960) recorded 1.59 HC (1 HC = 188.1 m) for a coenocline along a topographic moisture gradient, 600 - 900 m, in the Siskiyou Mountains, Oregon. Whittaker & Niering (1965, 1968) computed 0.92 HC (1 HC = 326.1 m) on limestone, 0.28 HC (1 HC = 1,071.4 m) on diorite and 3.14 HC (1 HC = 95.5 m) on granite-gneiss substrates along topographic-moisture gradients, 1,830 - 2,130 m, in the Santa Catalina Mountains, Arizona. Westman (1975a) recorded 2.3 HC for forest vegetation along a gradient in podzolization on sandy coastal terraces in northern California and Westman (1975b) recorded 0.6 HC (1 HC = 333 m) along a 200 m elevational transect through subtropical dune forest in Queensland. In Californian coastal sage there were 0.63 HC (1 HC = 135 km) along an environmental gradient from the coast to 85 km inland (Westman, 1981).

Correlation analysis

The three measures of alpha diversity were subjected to simple and stepwise multiple and partial correlation analysis in relation to 15 environmental and other variables. Matrices of simple correlation coefficients between all variables are given in Tables 4, 5 and 6 for the full data set, fynbos-renosterveld and forest-thicket communities respectively. The results of the multiple and partial correlation analyses are shown in Table 7.

Predictably many independent variables were highly colinear in all data sets. In the full data set (Table 4) species richness (\underline{S}) showed strong positive relationships with phytochorological diversity (PD), grazing intensity (GRZ), and negative relationships with litter (LIT) and average annual rainfall (RAI). Similar results were obtained for the fynbos and renosterveld communities (Table 5) where vegetation age (VAG) was also highly correlated with \underline{S} . In the forest and thicket communities (Table 6) \underline{S} was also strongly correlated with PD and RAI and showed a weaker negative relationship with percentage sand (SAN) and a positive relationship with rock cover (RCO). In all data sets there were no significant relationships between \underline{S} and variables reflecting soil fertility (cf. Grime, 1973; Huston, 1979; 1980).

Table 6. Correlation matrix for species diversity variables and various environmental and other variables. Forest and thicket communities ($n = 33$). See Table 1 and text for explanation of abbreviations.

[illegible]

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Fig. 1 shows the relationship of \underline{S} to PD. The correlation is stronger for the forest and thicket than the fynbos and renosterveld communities. Fig. 2 shows the relationship of \underline{S} to the two disturbance variables, VAG and GRZ, for grazed and fire-prone fynbos and renosterveld communities. When the renosterveld was treated separately, \underline{S} was not significantly correlated with both VAG and GRZ. In the fynbos communities disturbance is clearly implicated in the regulation of species richness (Campbell & Van der Muelen, 1980; Van Wilgen, 1980; Kruger, 1982). The relationship between \underline{S} and GRZ is curvilinear and the overall pattern supports the intermediate disturbance hypothesis (Connell, 1978) for which there is considerable empirical support from different ecosystems (Harper, 1969; Zeevalking & Fresco, 1977; Lubchenco, 1978; Naveh & Whittaker, 1979). The possibility of a spurious relationship between \underline{S} and both VAG and GRZ cannot be overlooked. For example there were no recently burnt or grazed plots in the S.E. Mountain Fynbos communities. I do not know what the effects of grazing or frequent burning would be on these communities. There are indications in S.W. Cape Mountain Fynbos that burning mature vegetation causes an increase in \underline{S} (Campbell and Van der Muelen, 1980) and Van Wilgen (1980) has reported richer stands in vegetation burnt on a short (6 yr) rotation than those with longer fire cycles. Much of the ambiguity results from combining different communities in the correlation analysis. I therefore examine later, for single fynbos and renosterveld communities, the response of diversity to different fire and grazing régimes.

In the full data set (Table 4) equitability ($\underline{H'}$) was highly correlated with \underline{S} and showed similar relationships to independent variables. $\underline{H'}$ increased with increasing vegetation age (VAG) but this does not necessarily contradict the generalization that equitability decreases with successional time (Auclair & Goff, 1971; Whittaker, 1969; 1972; 1977; Shafi & Yarranton, 1973; Houssard *et al.*, 1980; Westman, 1981). This relationship reflects the relatively higher values of $\underline{H'}$ for non fire-prone forest and thicket communities when compared to the frequently disturbed fynbos and renosterveld communities.

Measures of soil fertility such as sum of exchangeable cations (BAS) and total nitrogen (NIT), both highly intercorrelated, emerged as significant negative correlates with $\underline{H'}$ for the fynbos-renosterveld data; there was also a significant positive correlation with SAN (Table 5). These relationships draw attention to the lower equitability of renosterveld communities on the heavier, more fertile soils. In the forest and thicket data, $\underline{H'}$ and \underline{S} were highly colinear ($r = .83$; $p < .001$) and were correlated with similar suites of independent variables.

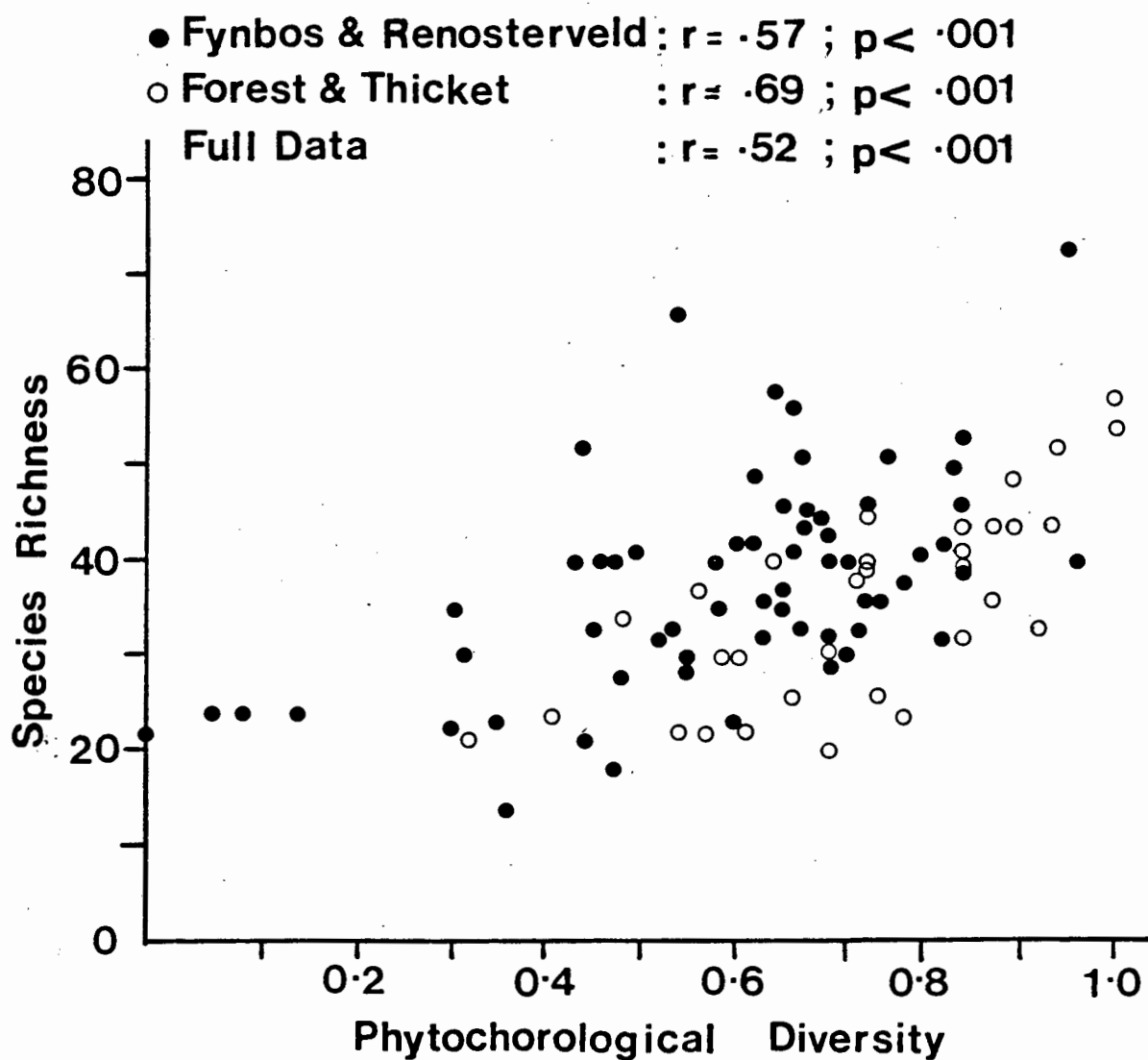


Fig. 1. Relationship of species richness to phytochorological diversity for fynbos and renosterveld ($n = 64$), forest and thicket ($n = 33$), and the full data set ($n = 97$).

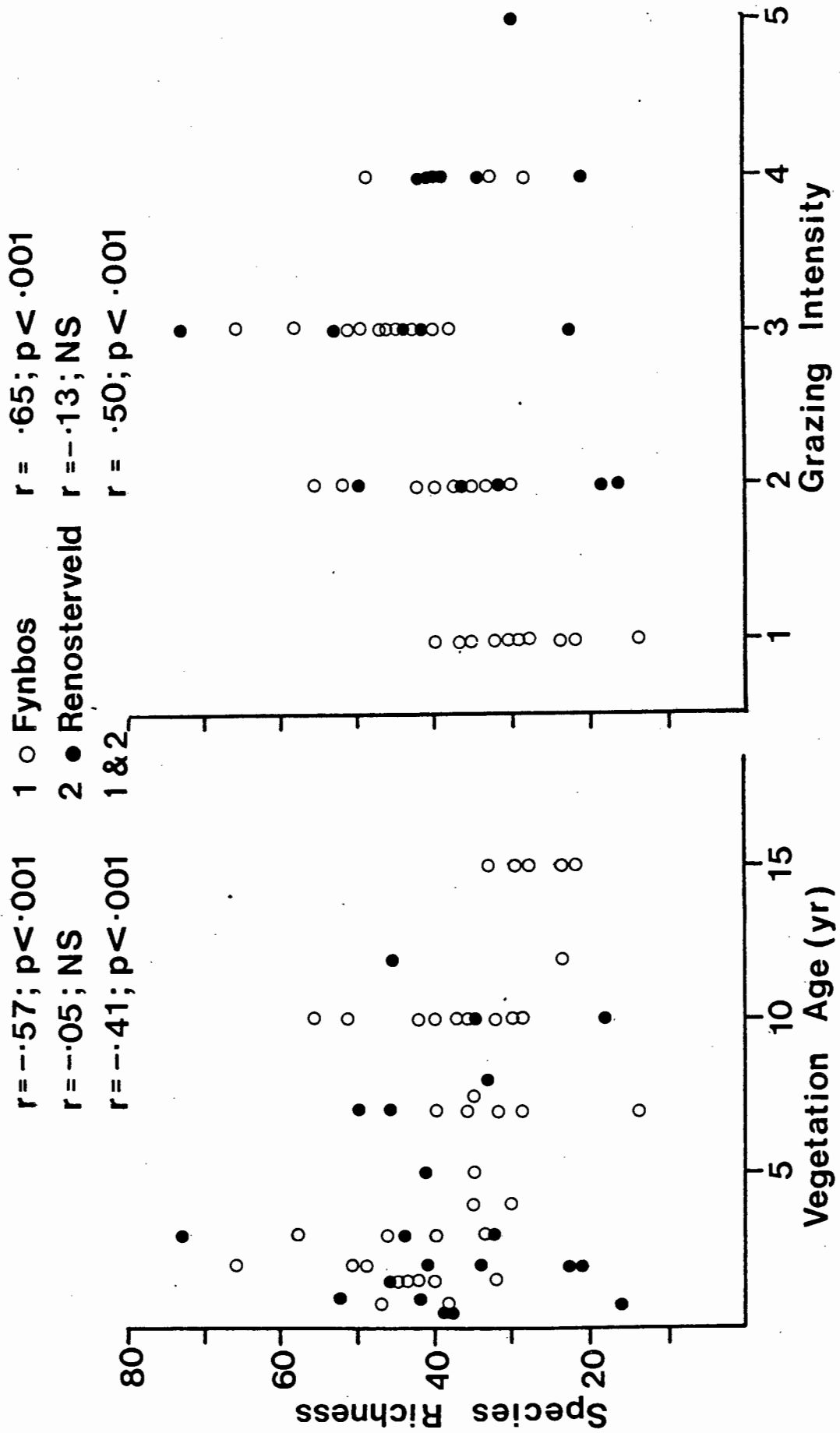


Fig. 2. Relationship of species richness to vegetation age and grazing intensity for fynbos ($n = 43$) and renosterveld ($n = 21$) communities.

Dominance concentration (\underline{C}) and $\underline{H'}$ were highly intercorrelated in all data sets ($r = -.92$; $r = -.93$; $r = -.89$ for full data, fynbos-renosterveld and forest thicket data sets respectively). Relationships are therefore the inverse of those with $\underline{H'}$.

The aim of the stepwise model was to isolate the minimum number of independent variables that contribute to explaining the variance of the diversity measures. The results of stepwise models are often difficult to interpret because of colinearity amongst "independent" variables. This problem was partly overcome since variables which were in approximately a linear combination with independent variables already in the model were not considered for entry into the model (Allen & Learn, 1973). Results of the stepwise models for all data sets are summarized in Table 7. With \underline{S} as the dependent variable, the amount of variance explained in the models ranged from 47% to 66%; in all analyses PD was entered into the models at the first step and contributed to the greatest reduction in variance (27% - 48%). GRZ reduced much variance of \underline{S} in the full data and fynbos renosterveld data sets while RCO emerged as an important independent variable in the forest-thicket data set. The models accounted for 40% - 61% of the variance of $\underline{H'}$ and only 32% - 39% of \underline{C} . Similar groups of variables were entered into the models for $\underline{H'}$ and \underline{C} in the different data sets. A greater proportion of the variance of all diversity measures was reduced in the data subsets than the full data.

Dynamics and disturbance

In this section I investigate the role of dynamics (succession) and disturbance (burning, mowing and grazing) in regulating species diversity in selected communities. Since different communities may respond to similar perturbations in different ways I determined the effects of grazing and burning/mowing on the diversity relations in a Grassy Fynbos and a renosterveld community.

A structural classification of these communities showed that they could be divided into two major structural cover states (cf. Slatyer, 1976). The Erica-Trachypogon Grassy Fynbos community comprises an ericoid shrub/grassy cover state which is burnt on a three to four yr rotation and is moderately grazed; and a proteoid shrub cover state which is burnt on a 10 to 12 yr rotation and is lightly grazed (Table 8). The former cover state had significantly more species per 100 m² plots than the latter; it also had higher values of $\underline{H'}$ and lower values of \underline{C} although these differences were not significant. Frequent burning and moderate grazing appear to increase species diversity in this and other Grassy Fynbos communities in the study area. There are certain compositional changes which

Table 7. Stepwise multiple and partial correlation analysis. See text and Table 1 for explanation of variable abbreviations. All variables are untransformed.

Dependent variables	Independent variables in order entered	R^2	Change in R^2	Significance level ¹	Partial r	Significance level
a) Full data ($n = 97$)						
S	PD	0.27	0.27	.000	.63	.000
	GRZ	0.42	0.15	.000	.44	.000
	PHH	0.45	0.03	.028	-.24	.017
	ASP	0.47	0.02	.058	-.20	.058
H ¹	VAG	0.16	0.16	.000	.43	.000
	PD	0.21	0.05	.010	.23	.027
	ALT	0.30	0.09	.001	.27	.009
	SAN	0.33	0.03	.038	.32	.002
	RAI	0.38	0.05	.010	-.24	.019
	PHH	0.40	0.02	.093	-.18	.093
C	VAG	0.12	0.12	.000	-.42	.000
	RCO	0.18	0.06	.010	-	-
	SAN	0.22	0.04	.030	-.34	.001
	ALT	0.25	0.03	.057	-.41	.000
	RAI	0.33	0.08	.002	.37	.000
	RCO-out ²	0.32	-0.01	.545		
b) Fynbos and renosterveld communities ($n = 64$)						
S	PD	0.32	0.32	.000	.69	.000
	GRZ	0.45	0.13	.001	.53	.000
	ASP	0.53	0.08	.005	-.27	.037
	BAS	0.59	0.06	.010	-.34	.007
	SAN	0.63	0.04	.017	-.31	.017
H ¹	SAN	0.14	0.14	.002	.52	.000
	PHH	0.26	0.12	.003	-	-
	RAI	0.32	0.06	.025	-.39	.002
	ALT	0.37	0.05	.026	.48	.000
	PHH-out	0.35	-0.02	.130	-	-
	GRZ	0.40	0.05	.030	.28	.030
C	SAN	0.15	0.15	.001	-.51	.000
	PHH	0.26	0.11	.004	-	-
	RAI	0.30	0.04	.070	.41	.001
	ALT	0.39	0.09	.005	-.49	.000
	PHH-out	0.38	-0.01	.305		
c) Forest and thicket communities ($n = 33$)						
S	PD	0.48	0.48	.000	.77	.000
	RCO	0.59	0.11	.009	.43	.015
	ALT	0.66	0.07	.035	.38	.035
H ¹	PD	0.33	0.33	.000	.67	.000
	RCO	0.55	0.21	.001	.56	.001
	ALT	0.61	0.06	.038	.38	.038
C	SAN	0.22	0.22	.006	.35	.052
	RCO	0.32	0.10	.044	-.37	.043
	PD	0.39	0.07	.079	-.32	.079

¹ Significance level at which variable entered the equation.

² Variable removed from equation by forward stepwise selection procedure.

Table 3. A comparison of diversity in 100 m² samples of two structural cover states in a Grassy Fynbos and a South Coast Renosterveld community in the study area.

	Erica-Trachypogon fynbos community		Themedia-Cliffortia renosterveld community	
	Ericoid shrub/grassy cover state n = 9	Proteoid shrub cover state n = 7	Mismanaged shrubland cover state n = 4	Well managed grass-land cover state n = 7
<u>Diversity variables</u>				
<u>S</u>	42.8 ± 6.4	36.6 ± 9.8*	31.3 ± 9.8	35.0 ± 7.9
<u>H'</u>	1.11 ± .08	1.04 ± 2.3	0.94 ± .23	0.59 ± .16**
<u>C</u>	0.12 ± .03	0.17 ± .17	0.18 ± .08	0.51 ± .10***
<u>Disturbance variables</u>				
<u>VAG</u> ¹	3.6 ± 2.4	11.4 ± 2.4	1.9 ± 1.0	2.2 ± .75
<u>GRZ</u> ¹	2.3 ± .71	1.7 ± .49	4.0 ± 0.0	3.1 ± .38
<u>Structural variables</u> (relative % cover)				
Proteoid shrubs ²	5.2 ± 6.7	16.2 ± 9.2	0.4 ± 0.4	0.0
Small-leaved shrubs ³	32.2 ± 14.8	47.5 ± 14.8	32.3 ± 11.4	4.5 ± 3.8
Grasses	38.8 ± 14.6	14.9 ± 11.4	37.1 ± 10.3	85.5 ± 6.4
Restioids ⁴	9.2 ± 7.8	10.1 ± 6.6	5.6 ± 5.5	1.3 ± 2.7

* $P < .1$; ** $P < .01$; *** $P < .001$

¹ See Table 1 for explanations of ₁ and classes within, these variables.

² Shrubs having isobilateral sclerophyllous leaves characteristic of the Cape Proteaceae.

³ Shrubs having leaves < 25 mm.

⁴ Restionaceae.

are not reflected in the diversity measures (Table 8). Frequent burning in fynbos communities often eliminates obligate reseeding species many of which are serotinous and cannot produce new propagules in the short intervals between fires (Bond, 1980; 1982; Campbell & Van der Muelen, 1980; Van Wilgen, 1980; Kruger, 1982). In the study area these include the proteoid shrubs, Protea neriifolia and P. repens. However, the elimination of these shrubs under a short fire cycle is more than compensated for by the post-fire invasion of many shade intolerant forbs and C₄ grasses which are suppressed under dense proteoid shrub canopy.

The Themeda-Cliffortia community is a wet renosterveld on seasonally waterlogged duplex soils and exists in a small-leaved shrub or grassland cover state (Table 8). The shrub state is derived from the grassland as a consequence of severe and prolonged overgrazing which reduces grass vigour and basal cover, and results in soil capping, increased run-off and eventually the disturbance of water table dynamics (Cowling, 1982a). There ensues a thickening up of relatively deep rooted small-leaved shrub species (e.g. Cliffortia linearifolia, Elytropappus rhinocerotis) which are able to exploit subsoil moisture, unavailable to the shallow rooted grasses. Table 8 shows that there is a slight, but insignificant reduction of \underline{S} in the shrubland cover state relative to the grassland; the latter had significantly lower values of \underline{H}^1 and higher values of \underline{C}^1 . The grassland is overwhelmingly dominated by a single grass species, Themeda triandra, but has many other grasses, forbs, geophytes and small-leaved shrubs (including those which dominate in the shrubland state), which contribute little to overall cover. Disturbance of the grassland results in reduced dominance concentration and increased equitability as species importance is more evenly distributed as the shrubs cover increases. However overall composition and richness do not change much although certain grasses are eliminated in the shrubland state.

Next I investigated diversity trends along a successional and grazing intensity gradient in communities on coastal dunes (Fig. 3). The successional communities are contemporary and therefore not strictly sequential. I was careful to select only plots on deep, well-drained sand from a climatically homogeneous area where vegetation ultimately develops, Clementsian-style, into a dense dune thicket. However, there is no certainty that pre-climax stages will actually follow this sequence. The assumption that spatially separate vegetation represents states of the same system at different stages of development has been criticized (Drury & Nisbet, 1973; Goodall, 1977). On the dunes and in the renosterveld and fynbos communities mentioned below, this assumption is borne out by

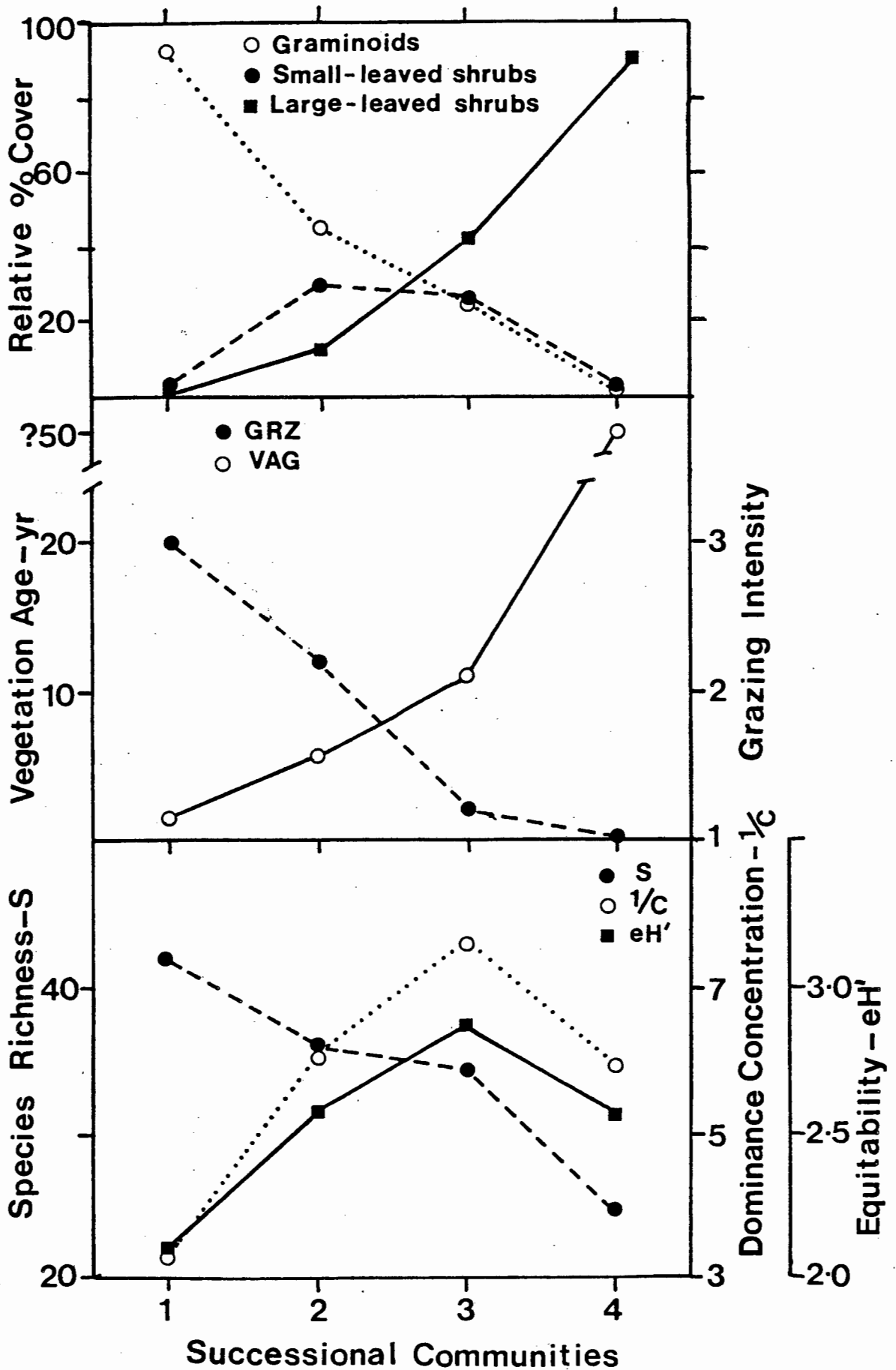


Fig. 3. Trends in diversity measures for dune communities along a gradient of decreasing grazing intensity and increasing vegetation age. Successional communities are: 1 - *Themeda Stenotaphrum* ($n = 2$); 2 - *Restio-Agathosma* ($n = 6$); 3 - *Restio-Maytenus* ($n = 9$); 4 - *Cassine-Cussonia* ($n = 8$).

fenceline contrasts separating different (structural) communities on identical sites (Cowling, 1982a). On the dunes the only physical site variable to show a consistent trend along the gradient was an increase in soil organic content due largely to a build-up in decomposition products from litter accumulated in the more mature communities.

The successional communities, ranged along the gradient of increasing vegetation age and decreasing grazing intensity, were a restioid grassland (Themeda-Stenotaphrum), dune fynbos (Restio-Agathosma), mixed dune fynbos-thicket (Restio-Maytenus) and the climax dune thicket (Cassine-Cussonia) (Fig. 3). The relative importance of graminoids decreased, and large-leaved shrubs increased, along the gradient while small-leaved shrubs showed a mid-successional peak. Richness decreased monotonically along the gradient and equitability increased to a maximum in the preclimax stage and then declined. Dominance concentration, expressed as $1/\underline{C}$, showed exactly the inverse trend of \underline{H}' . (Fig. 3).

Many studies show a mid-successional peak in diversity followed by a reduction associated with the competitive elimination of non-climax species in the climax stage. The mid-successional peak is attributed to the coexistence of early and late successional species in a single stand (Loucks, 1970; Auclair & Goff, 1971; Shafi & Yarranton, 1973; Whittaker, 1972; 1977; Westman, 1975b) and that in many landscapes the mid-successional stage is most frequent within the successional mosaic (Loucks, 1970; Denslow, 1980). Increase of species diversity from successional stages to the climax is often observed (Monk, 1967; Reiners et al., 1971; Nicholson & Monk, 1974) and has been stated as a generalization (Margalef, 1963; Odum, 1969). At least one study has reported a steady decrease in diversity after initial post-fire establishment (Habeck, 1968).

The decline in diversity of the dune communities towards the terminal climax is probably associated with the dominance of the community by large-leaved shrubs and the closure of the canopy (cf. Auclair & Goff, 1971; Peet, 1978; Houssard et al., 1980; Westman, 1981). The mid-successional peak in \underline{H}' coincides with the roughly equal representation of graminoids, small- and large-leaved shrubs (Fig. 3). The high richness of the grassland community could be the result of a higher grazing intensity and frequent mowing allowing the establishment and persistence of certain species which are not found in the other communities (Maarel, 1971). High \underline{C} is explained by the dominance of Stenotaphrum secundatum, a grass which forms an extensive, dense turf under conditions of frequent mowing and grazing.

Discussion

Global comparisons

Our understanding of intercontinental diversity patterns is still in a rudimentary phase and is plagued by a number of conceptual problems, most of which have been discussed succinctly by Rice & Westoby (1982a). Convergence theory predicts that in genetically isolated habitats sharing similar environments, overall community structure would be similar (Cody & Mooney, 1978). This theory assumes that species richness is at equilibrium in evolutionary time and can be interpreted largely in terms of ecological processes. Comparisons of species richness in mediterranean climate regions of the world (Whittaker, 1977; Naveh & Whittaker, 1979; Cowling & Campbell, 1980; Westman, 1981) and other globally comparable biome-types (Shmida & Whittaker, 1979; Rice & Westoby, 1982a) have shown important differences in species richness among analogous vegetation types on different continents. Historical differences are usually invoked to explain this non-convergence: for example Whittaker (1977) and Naveh & Whittaker (1979) attribute the higher richness of the southern hemisphere "mediterranean" heathlands, when compared to their shrubland (sensu Di Castri, 1980) "analogues", to the longer evolutionary histories of the heathland floras. Clearly this hypothesis refutes the notion of a global equilibrium or saturation of species richness (Rice & Westoby, 1982a).

I concur with Rice & Westoby (1982a) that the level or scale of diversity is of paramount importance for global comparisons. Naveh & Whittaker (1979) cite data from 0.1 ha samples (alpha richness) as evidence for the high diversity of Cape Fynbos. My data indicates that at this scale (Table 2) fynbos is no richer than other shrublands, some of which (e.g. subtropical thicket) certainly have not had a long history in their present area (Cowling, 1982b). The similarly high richness of certain fynbos communities and subtropical grassland on infertile soils (Table 2) indicates that ecological factors such as low levels of available soil nutrients could be implicated in the regulation of diversity at this scale (Campbell & Cowling, 1980; Rice & Westoby, 1982a). Kruger & Taylor (1979) observe that in sites of about 1.0 km^2 and less, South African grassland and savanna have approximately as many species as do Cape fynbos sites of equal size. However they recorded exceptionally high levels of delta diversity. Perhaps the turnover in species composition along analogous landscape gradients or within analogous habitats (Cody, 1982) on different continents are more appropriate diversity scales for global comparisons.

A further point raised by Rice & Westoby (1982a) is the difficulty of defining analogous vegetation types which might be expected to converge. I seriously question the validity of comparing renosterveld with both mesic, evergreen and xeric, drought deciduous mediterranean shrublands (Westman, 1981) on other continents. Throughout its climatic range (where rainfall varies from 300 - 600 mm yr⁻¹) renosterveld is dominated by evergreen, small-leaved, sclerophyllous or semi-succulent shrubs and much of the South Coastal Renosterveld is derived, in historic times, from grasslands. Axelrod (1978) postulates that California coastal sage scrub is similarly grassland-derived although Westman (1981) argues against this assertion. Furthermore, unlike other mediterranean regions, the Cape mediterranean climate zone is not isolated from the humid subtropical rainfall region but grades into it along the S.E. and S. Cape coastal forelands, thus allowing for the penetration of subtropical elements. This amounts to a great deal of phytochorological mixing which, as I will argue in a later section, has important implications for renosterveld species richness.

Perhaps the situation is not so bad that "global variation in floristic richness appears best explained by historical and biogeographic events specific to each region" (Westman, 1981). That historic events act as constraints to convergence cannot be ignored (Cody & Mooney, 1978). However a deeper understanding of global patterns of plant species richness will emerge once we understand the factors controlling the different levels of diversity in each region. The remainder of this paper is devoted towards this end for the S.E. Cape.

Diversity patterns in the study area: within Cape comparisons

In this section I discuss patterns of diversity in the study area communities in relation to current generalizations concerning Cape fynbos diversity. Both Taylor (1978) and Kruger (1979) have stated that strikingly high alpha richness and equitability are general features of fynbos communities.

My data does not support these generalizations. The highest richness in Tables 2 and 3 were recorded in renosterveld communities and highest equitability in thicket. There is a trend for renosterveld to have lowest values of H' and highest of C although high values of C (e.g. 0.51) were recorded in some fynbos plots.

Beta diversity in Cape fynbos is also supposedly high (Campbell & Van der Muelen, 1980). I have shown that there are 1.6 more half-changes in non-fynbos than fynbos along comparable environmental gradients. Although these data could be taken as evidence refuting the generalization of higher beta diversity in fynbos relative to other vegetation types, some further explanation is required. The S.E. Cape is an area of steep environmental gradients and forms a convergence zone for four African phytochoria (Cowling, 1982a). Vegetation types change rapidly over very short distances. Under these conditions a high beta diversity is to be expected. The non-fynbos coenocline ranges from Tongaland-Pondoland thicket (Moll & White, 1978) with a strong karrooid component, to mesic Afromontane forest and transcends a phytochorological boundary over a distance of 500 m. The distribution of fynbos is determined more by infertile soils than climate (Taylor, 1978; Kruger, 1979) and no phytochorological boundary was transcended along the fynbos coenocline, where soils were all infertile.

Phytochorological complexity and tension zones

Biogeographic relations can have a significant influence on species diversity as they determine historic differences in the availability of species from different areas (Whittaker, 1972; Danin, 1978). Past climatic changes result in shifts of the boundaries of phytochoria causing contacts with different floras which may increase the number of species in certain environments.

In the study area an index of phytochorological diversity (PD) emerged as the variable most significantly correlated with species richness in all data sets (Table 7). The S.E. Cape is a complex tension zone where species characteristic of at least four phytochoria contribute to the richness of phytochorologically mixed communities. Danin (1978) and Naveh & Whittaker (1979) recorded high species richness in the most biogeographically complex regions of their study areas in the Middle East. Westman (1981) noted the highest increase in diversity in California coastal sage communities where a mixing of southern and northern floras occurs. Bond (1981) found that the richest communities (waboomveld) in the southern Cape mountains occurred on the ecotone between renoster-veld and fynbos and had a diverse assemblage of fynbos shrubs and graminoids, karrooid shrubs, and subtropical grasses.

The S.E. Cape comprises a transition zone between the warm temperate winter rainfall region and the subtropical summer rainfall region. Generally the rainfall distribution is bimodal with spring and autumn maxima although it is highly variable with winter a peak one year and a summer peak the next (Schulze, 1965; Gibbs Russel & Robinson, 1981). It has been shown (Roux, 1966) that in the mixed grass-karroid shrub communities of the region, grass growth is favoured by summer rains and shrubs by winter rains: farmers speak of "grass" years and "bush" years. This transitional and variable rainfall régime allows species of diverse biogeographical affinities to coexist in single stands and facilitates high alpha richness since there are a wide range of conditions for germination, establishment and growth (Grubb, 1977; Pierce & Cowling, 1982).

PD is negatively correlated with the colinear variables of average annual rainfall (RAI) and altitude (ALT), and is positively correlated with soil pH (PHH), available calcium (CAC) and sum of exchangeable bases (BAS), an interrelated group of variables reflecting soil fertility (Table 4). In the study area chorologically mixed communities are confined to drier lowland communities on fertile to moderately infertile soils (e.g. thickets, renosterveld, dune fynbos and certain grassy fynbos communities). Mesic fynbos communities on highly infertile soils (e.g. S.E. Mountain Fynbos and the Thamnochortus-Erica Grassy Fynbos community) have low values of PD and low species richness. The mesic, high altitude Afromontane forest communities show similarly low patterns of PD and S.

Generally there is a greater phytochorological mixing in drier communities with more fertile soils; mesic communities which have an adequate and predictable rainfall, and, in fynbos, have highly infertile soils, are phytochorologically pure and species-poor. I comment further on the effect of soil nutrients on phytochorological mixing and richness in a later section.

Equilibrium biogeography versus history

In the S.E. Cape, Mountain Fynbos and Afromontane forests have patchy or island-like distributions within a continental setting. It is therefore possible to invoke island biogeography theory to explain the diversity patterns of these vegetation types. In this section I present, as alternatives, an ecological and an historical hypothesis to explain the richness of Mountain Fynbos and Afromontane forest communities in the study area.

In the S.E. Cape, Mountain Fynbos is pinched into an eastwardly narrowing peninsula on the upper slopes of the higher mountains, which is separated from the "mainland source area" of the mesic coastal mountains by a wide belt of inhospitable terrain. Afromontane forest is patchily distributed in an archipelago of mountain islands throughout the African continent (White, 1978). In the study area these forests are confined to small patches on deep colluvial soils in the cool, wet parts of the Elandsberg Mountains and are isolated from the large contiguous block of forests in the Knysna region to the west. Cody (1982) has demonstrated the significance for bird diversity of the patchy distribution of Afromontane forests west of the Knysna region.

Central to the theory of island biogeography is the assumption that present day ecosystems are in an equilibrium state (MacArthur & Wilson, 1967; MacArthur, 1972). If one assumes ecological saturation it is permissible largely to ignore historical events (Pianka, 1966; Vuilleumier & Simberloff, 1980) and explore the great potential for modelling, predicting and interpreting diversity (MacArthur, 1972). Assuming a dynamic equilibrium between species immigration and extinction, mediated by competitive interactions in ecological time, it is possible to predict the species numbers on a given island by means of a conveniently small number of easily measured environmental variables such as distance from the mainland source and island area (Johnson *et al.*, 1968; Johnson & Raven, 1968; Simpson, 1974; Nilsson & Nilsson, 1978).

The predictions of island biogeography theory afford a reasonable explanation for the low richness of Mountain Fynbos and Afromontane Forest patches in the study area. In the small areas occupied by these vegetation types there may be few habitat types and a tendency for higher extinction rates due to smaller population sizes than on the larger contiguous areas that constitute the "mainland" source. I have shown that alpha richness of Mountain Fynbos communities of the Outeniqua mountains to the west (part of the "mainland") is higher than in the study area. It would be desirable to have richness data from the contiguous Knysna Afromontane forests.

An important tenet of island biogeography theory is density compensation which predicts that a given species would be more abundant and have a broader niche on a species-poor island than on an adjacent species-rich mainland (MacArthur *et al.*, 1972). It would be of interest to test whether species shared by the "mainland" Mountain Fynbos communities (e.g. in the Tsitsikamma Mountains) and the "island" communities of the study area, have greater habitat breadth in the latter area when investigations are carried out along comparable environmental gradients in both sites.

In recent years island biogeography theory has been criticized both from a theoretical (Whittaker, 1977; Connor & McCoy, 1979; Connor & Simberloff, 1979) and an empirical basis (Vuilleumier & Simberloff, 1980; Weaver & Kellman, 1981). There has been much criticism of the equilibrium assumption for plant communities: the difficulty of explaining competitive niche diversification in species-rich plant communities and also the notion that disturbance in the long term (climatic change) and the short term (fire, grazing, landslides, etc.) results in continuous changes in the competitive hierarchy (Connell, 1978; Huston, 1979). Geographical ecology has been criticized for not fully appreciating the impact of historical factors (Sieb, 1980; Vuilleumier & Simberloff, 1980) even though these are often poorly understood and not amenable to conclusive tests (Pianka, 1966; Cody, 1982). I present below an alternative historical hypothesis which does not assume equilibril conditions, to explain the richness of Afromontane forest and Mountain Fynbos in the study area.

There is a growing body of data to suggest that Pleistocene glacial climates were both colder and drier in the Cape coastal region than present Holocene interglacial conditions (Deacon, 1982). Therefore during the last glacial, Afromontane forest would have been largely eliminated from the study area and it is possible that only a few relic patches survived in the Knysna region (Cowling, 1982b). Mountain Fynbos would have been restricted to even smaller patches on the mountains (Cowling, 1982b). With the onset of warmer wetter conditions after about 12,000 B.P. (Deacon, 1982), the areal extent of both vegetation types would have expanded and communities would have been enriched by the immigration of new species from relics. It could be argued that the relatively low richness of Mountain Fynbos and Afromontane Forest in the study area is because too little time has elapsed since climatic amelioration for many species to disperse from the source areas to the expanding "islands" (cf. Taylor & Regal, 1978; Vuilleumier & Simberloff, 1980). It is hard to envisage the establishment of equilibril conditions in plant communities under the continuously changing climate of a glacial-interglacial sequence.

There are problems with both hypotheses. The ecological theory is certainly more testable but it would be very difficult in practice to evaluate the respective roles of the absence of required ecological habitat and competition as factors regulating the richness of "island" floras - we simply lack the required autecological information. Historical hypotheses are difficult to test and the model of climatic change used to predict vegetation changes in the study area is very rudimentary (Deacon, 1982).

Dynamics and disturbance

There has been a surge of interest in non-equilibrium models of species diversity (e.g. Caswell, 1978; Connell, 1978; Huston, 1979) arising from the notion that the "frequencies of natural disturbance ... are often much faster than the rate of recovery from perturbations" (Connell, 1978). In this section I discuss the role of short term disturbances (fire, grazing) as factors which regulate species diversity in the study area.

Connell (1978) and Huston (1979) postulate a dynamic model of species diversity: in the absence of disturbance mediated population reduction, a competitive equilibrium results with one or few species dominating and diversity is low; at high frequencies of population reduction only those species capable of reproducing under the heavy disturbance regime will persist, and diversity will also be low. Species diversity will be highest at an intermediate disturbance level, at which most species can co-exist.

Fig. 2 supports the intermediate disturbance hypothesis for the relationship between grazing intensity and species richness in fynbos communities. Disturbance, in the form of frequent fires, enhances species richness in fire-prone fynbos shrublands (Fig. 2, Table 5). In fynbos, much of the patch area at any given time is in the form of large-scale clearings after fire. The high richness in the youthful post-fire stage could be because most species are adapted for establishment in open, high-light intensity post-fire conditions and many are suppressed and do not reproduce successfully as the community matures and the canopy closes (cf. Loucks, 1970; Whittaker & Levin, 1977; Denslow, 1980). I did not observe similar patterns in the equally fire-prone renosterveld communities.

On the coastal dunes I demonstrated a trend of decreasing richness associated with gradients of decreasing grazing intensity and increasing vegetation age and thicket development (Fig. 3). However, certain thicket communities which have remained relatively undisturbed for decades or even centuries, are very rich and have the highest equitability in the study area (Table 3). It seems that recurrent large scale disturbances such as fire are not implicated in the regulation of diversity in these communities. In the drier thicket a variable soil moisture supply has allowed for the coexistence of a diverse flora of shallow-rooted succulents with deep-rooted, evergreen, sclerophyllous subtropical shrubs and trees. The latter component comprises species which nearly all produce fleshy, bird-dispersed fruits. Fruiting periods are highly variable within and among species (Pierce & Cowling, 1982) and therefore the proportion of viable seed of different

species available to recolonize small disturbance patches (e.g. landslide, occasional shrub death, or elephant damage in pre-colonial times) will show appreciable temporal and spatial variability. This asynchronism in fruit production and dispersal may represent a way to limit competition (Grubb, 1977; Houssard *et al.*, 1980) and thus account for the relatively high alpha diversity in thicket.

The role of soil nutrients

Huston (1979) has presented a non-equilibrium hypothesis of species diversity that predicts, amongst other things, high diversity on infertile substrates. He argues that slow growth rates on these stressed sites would "reduce the rate of competitive displacement allowing a longer period of coexistence among competitors and thus the maintenance of diversity" (Huston, 1979; see also McNaughton, 1967; Grime, 1973; 1977; Newman, 1973). There is much experimental evidence to show that the fertilization of pastures on infertile soils results in an increase of standing crop and a reduction in diversity (e.g. Willis, 1963; Jeffrey & Piggot, 1973). Huston (1980) found strong correlations between species richness of Costa Rican forests and low levels of soil nutrient availability and other factors which would reduce growth rates. Some studies show an increase in plant diversity with increasing soil fertility (e.g. Monk, 1967; Westman, 1975a; Whittaker, 1977).

My data would appear to falsify Huston's (1979) hypothesis. Fynbos communities on the least fertile soils (Mountain Fynbos, Thamnochortus-Erica community) have low diversity whereas thicket on the most fertile soils can have very high diversity (Tables 2 and 3). In the correlation analysis measures of soil fertility were not significantly correlated with species richness (S) in all data sets and there were some significant negative correlations between soil nutrients and equitability (H') (Tables 4 - 6). It could be argued that the highly infertile fynbos soils represent a case of extreme deficiency and would therefore support species-poor communities (Grime, 1973; Huston, 1979; 1980). However these soils are comparable to, if not slightly more fertile than, fynbos soils of the S.W. Cape (Campbell, 1982) which support species-rich communities. The relatively high diversity of thicket, which grows on fertile soils, is unexplained by Huston's (1979) theory.

In the S.E. Cape fynbos, highly leached infertile soils are an edaphic barrier for the migration of species from non-Cape phytochoria (e.g. subtropical grasses), and they support communities of low phytochorological diversity and richness (see below).

When the 27 samples of Grassy Fynbos and Mountain Fynbos on T.M.G. quartzites were treated separately, there were significant positive correlations between \underline{S} and available phosphorus ($\underline{r} = .56$; $\underline{p} < .01$), total nitrogen ($\underline{r} = .42$; $\underline{p} < .02$), sum of exchangeable bases ($\underline{r} = .47$; $\underline{p} < .02$) and pH ($\underline{r} = .48$; $\underline{p} < .02$). The generally highest diversities in the study area were recorded in dry renosterveld communities on moderately fertile soils where conditions appeared suitable for the establishment, growth and persistence of species from a wide range of phytocorological groups.

Other hypotheses

Many explanations for diversity patterns have been proposed. In this section I discuss briefly the importance of some hypotheses, not already discussed below, in explaining diversity relations in the study area.

My data are consistent with other studies (e.g. McNaughton, 1967; Risser & Rice, 1971; Whittaker, 1972; 1977; Grime, 1973; Whittaker & Niering, 1975; Glenn-Lewin, 1977; Naveh & Whittaker, 1979) in giving no support to the productivity hypothesis (Connell & Orias, 1967), if annual average rainfall can be taken as a rough index of productivity potential. Maximum diversity was not recorded in the most mesic or favourable environments (cf. Terborgh, 1973; Richardson & Lum, 1980).

The relationship between diversity and stability has received considerable attention in the past (see Whittaker, 1977 for a review) and is usually confounded by conflicting definitions of stability (Orias, 1975; Whittaker, 1975). Environmental instability, expressed as a greater temporal heterogeneity of water supply and temperature régime in the valley climate of the study area, has promoted species diversity in thicket communities by permitting the coexistence of a variety of growth forms specialized in different ways to the irregular availability of water and great diurnal and annual temperature ranges (cf. Whittaker & Niering, 1975; Whittaker, 1977). Unstable, non-equilibrium conditions maintained in fynbos communities by periodic fires are important in regulating diversity. Long term climatic instability is an important factor in regulating the diversity of S.E. Cape vegetation where climatic change has altered biogeographic boundaries and promoted phytocorological mixing.

Other measures of environmental heterogeneity are frequently correlated with plant species diversity (Pianka, 1966; Harner & Harper, 1976; Grubb, 1977; Ricklefs, 1977; Houssard *et al.*, 1980). Richness (\underline{S}) and equitability ($\underline{H'}$) showed a weak positive correlation with rock cover (RCO) for the forest-thicket communities (Table 6) but was not significantly correlated in the other data sets.

Concluding remarks

No single hypothesis discussed in this paper could adequately explain diversity relations in all vegetation types studied. Phytochorological diversity emerged as a consistently significant correlate in all data sets. However this factor is probably an unimportant predictor of plant species diversity outside tension zones. Species-rich S.W. Cape fynbos and tropical lowland forest communities will have low values of phytochorological diversity.

More of the variance in species diversity was explained when the full data set was subdivided into two groups of biogeographically and structurally related communities. Even more variance was explained when one or few related communities on the same parent material and having similar mesoclimates were subjected to multiple correlation analysis (Cowling, in preparation). Perhaps it is too ambitious to seek unifying patterns in very heterogeneous data sets.

It is difficult to untangle the complex of factors which have influenced the evolution and maintenance of diversity in any given region, let alone make generalizations on a global scale. It is clear to me that historical factors should not be merely treated as "noise" or the substance of *ad hoc* explanations when ecological theories fail. Although ecological theories often yield more, and better defined, predictions than historical explanations, the latter should be considered at all stages of a study. In many cases ecological and evolutionary time cannot be realistically separated in their effects on community structure (Whittaker, 1977; Vuilleumier & Simberloff, 1980). In my study area historical events such as climate change and phytochorological mixing, and ecological factors such as fire, grazing, soil nutrients, phenology and climate have all contributed to the evolution and maintenance of diversity in one or more communities at all times.

References

- Acocks, J.P.H., 1953. Veld types of South Africa. *Mem. Bot. Surv. S. Afr.* 28.
- Allen, J. & Learn, J., 1973. STEPREG 1: Stepwise linear regression analysis. Reference manual. Academic Computing Centre, Madison, 51 pp.
- Anon., 1942. Weather on the coasts of southern Africa. Part 3. Union of South Africa from Mossel Bay to East London. Government Printer, Pretoria, 52 pp.
- Auclair, A.N. & Goff, F.G., 1971. Diversity relations of upland forests in the western Great Lakes area. *Amer. Natur.* 105: 499 - 528.
- Axelrod, D.I., 1978. Origin of coastal sage vegetation, Alta and Baja California. *Amer. J. Bot.* 65: 1117 - 1131.
- Bond, W.J., 1980. Fire and senescent fynbos in the Swartberg, southern Cape. *S. Afr. For. J.* 114: 68 - 71.
- Bond, W.J., 1981. Vegetation gradients in the southern Cape mountains. Unpublished thesis, University of Cape Town.
- Bond, W.J., 1982. Fire and serotiny in Cape Proteaceae. Unpublished ms.
- Boucher, C., 1978. Cape Hangklip area. II. The vegetation. *Bothalia* 12: 455 - 497.
- Boucher, C. & Moll, E.J., 1980. South African mediterranean shrublands. In: F. di Castri, D.W. Goodall, & R.L. Specht (eds.), *Mediterranean-type shrublands*, p. 233 - 248. Elsevier, Amsterdam.
- Campbell, B.M., 1982. Montane plant environments of the Fynbos Biome. Submitted to *Bothalia*.
- Campbell, B.M. & Moll, E.J., 1977. The forest communities of Table Mountain, South Africa. *Vegetatio* 34: 105 - 115.
- Campbell, B.M. & Van der Muelen, F., 1980. Patterns of plant species diversity in fynbos vegetation, South Africa. *Vegetatio* 43: 43 - 47.
- Campbell, B.M., Cowling, R.M., Bond, W.J. & Kruger, F.J., 1981. Structural characterization of vegetation in the Fynbos Biome. *S. Afr. Nat. Sci. Prog. Rep.* 53. CSIR, Pretoria.
- Caswell, H., 1978. Predator-mediated coexistence: a nonequilibrium model. *Amer. Natur.* 112: 127 - 154.
- Cody, M.L., 1982. Continental diversity patterns and convergent evolution in bird communities. In: F.J. Kruger, D.T. Mitchell & J.U.M. Jarvis (eds.), *Mediterranean-type ecosystems. The role of nutrients*. Springer, Berlin, Heidelberg, New York (in press).
- Cody, M.L. & Mooney, H.A., 1978. Convergence versus non-convergence in mediterranean-climate ecosystems. *Ann. Rev. Ecol. Syst.* 9: 265 - 321.
- Connel, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302 - 1310.

- Connell, J.H. & Orias, E., 1964. The ecological regulation of species diversity. *Amer. Natur.* 98: 399 - 414.
- Connor, E.F. & McCoy, E., 1979. The statistics and biology of the species-area relationship. *Amer. Natur.* 113: 791 - 833.
- Connor, E.F. & Simberloff, D., 1979. The assembly of species communities: chance or competition? *Ecology* 60: 1132 - 1140.
- Cowling, R.M., 1982a. A syntaxonomic and synecological study in the Humansdorp region of the Fynbos Biome. Submitted to *Bothalia*.
- Cowling, R.M., 1982b. Phytosociology and vegetation history in the south eastern Cape, South Africa. Submitted to *J. Biogr.*
- Cowling, R.M. & Campbell, B.M., 1980. Convergence in vegetation structure in the mediterranean communities of California, Chile and South Africa. *Vegetatio* 43: 191 - 197.
- Cowling, R.M. & Campbell, B.M., 1982. A comparison of fynbos and non-fynbos coenoclines in the lower Gamtoos River Valley, south eastern Cape, South Africa. Submitted to *Vegetatio*.
- Danin, A., 1978. Plant species diversity and ecological districts of the Sinai Desert. *Vegetatio* 36: 83 - 93.
- Deacon, H.J., 1982. The comparative evolution of mediterranean-type ecosystems: a southern perspective. In: F.J. Kruger, D.T. Mitchell & J.U.M. Jarvis (eds.), *Mediterranean-type ecosystems. The role of nutrients*. Springer, Berlin, Heidelberg, New York (in press).
- Denslow, J.L., 1980. Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia* 46: 18 - 21.
- Di Castri, F., 1980. Mediterranean-type shrublands of the world. In: F. di Castri, D.W. Goodall & R.L. Specht (eds.), *Mediterranean-type shrublands*, p. 1 - 52. Elsevier, Amsterdam.
- Draper, N.R. & Smith, H., 1966. *Applied regression analysis*. Wiley, New York.
- Drury, W.H. & Nisbet, I.C.T., 1973. Succession. *J. Arnold Arboretum* 54: 331 - 368.
- Eiten, G., 1978. Delimitation of the cerrado concept. *Vegetatio* 36: 169 - 178.
- George, A. S., Hopkins, A.J. & Marchant, N.G., 1979. The heathlands of Western Australia. In: R.L. Specht (ed.), *Heathlands and related shrublands of the world, A. Descriptive studies*, p. 211 - 230. Elsevier, Amsterdam.
- Gibbs Russell, G.E. & Robinson, E.R., 1981. Phytogeography and speciation in the vegetation of the eastern Cape. *Bothalia* 13: 467 - 472.
- Glenn Lewin, D.C., 1977. Species diversity in North American temperate forests. *Vegetatio* 33: 153 - 162.
- Goodall, D.W., 1977. Dynamic changes in ecosystems and their study: the roles of induction and deduction. *J. Environ. Mgmt.* 5: 309 - 317.

- Grime, J.P., 1973. Competition and diversity in herbaceous vegetation. *Nature* 244: 311.
- Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary history. *Amer. Natur.* 111: 1169 - 1194.
- Grubb, P.J., 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52: 107 - 145.
- Habek, J.R., 1968. Forest succession in the Glacier Park cedar-hemlock forests. *Ecology* 49: 872 - 880.
- Harner, R.F. & Harper, K.T., 1976. The role of area, heterogeneity and favourability in plant species diversity on Pinyon-Juniper ecosystems. *Ecology* 57: 1254 - 1263.
- Harper, J.L., 1969. The role of predation in vegetational diversity. *Brookhaven Symp. Biol.* 22: 48 - 62.
- Hill, M.O., 1973a. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54: 427 - 432.
- Hill, M.O., 1973b. Reciprocal averaging: an eigenvector method of ordination. *J. Ecol.* 61: 237 - 249.
- Hnatiuk, R.J. & Hopkins, A.J.M., 1981. An ecological analysis of kwongan vegetation south of Eneabba, Western Australia. *Austr. J. Ecol.* 6: 423 - 438.
- Houssard, C., Escarre, J. & Romone, F., 1980. Development of species diversity in some Mediterranean plant communities. *Vegetatio* 43: 59 - 72.
- Huston, M., 1979. A general hypothesis of species diversity. *Amer. Natur.* 133: 81 - 101.
- Huston, M., 1980. Soil nutrients and tree species richness in Costa Rican forests. *J. Biogeogr.* 7: 147 - 158.
- Jeffrey, D.W. & Piggot, C.D., 1973. The response of grasslands on sugar-limestone in Teesdale to application of phosphorus and nitrogen. *J. Ecol.* 61: 85 - 92.
- Johnson, M.P. & Raven, P.H., 1970. Natural regulation of plant species diversity. *Evol. Biol.* 4: 127 - 162.
- Johnson, M.P., Mason, L.G. & Raven, P.H., 1968. Ecological parameters and plant species diversity. *Amer. Natur.* 102: 297 - 306.
- Kruger, F.J., 1978. A description of the Fynbos Biome Project. *S. Afr. Nat. Sci. Progr. Rep.* 28. CSIR, Pretoria.
- Kruger, F.J., 1979. South African heathlands. In: R.L. Specht (ed.), *Heathlands of the world. A. Descriptive studies*, p. 19 - 80. Elsevier, Amsterdam.
- Kruger, F.J., 1982. Plant community diversity and dynamics in relation to fire. In: F.J. Kruger, D.T. Mitchell, & J.U.M. Jarvis (eds.), *Mediterranean-type ecosystems. The role of nutrients*. Springer, Berlin, Heidelberg, New York (in press).

- Kruger, F.J. & Taylor, H.C., 1979. Plant species diversity in Cape fynbos: gamma and delta diversity. *Vegetatio* 47: 85 - 93.
- Lamont, B., Downes, S. & J.E.D. Fox, 1977. Importance value curves and diversity indices applied to species-rich heathland in Western Australia. *Nature* 265: 438 - 441.
- Loucks, O.L., 1970. Evolution of diversity, efficiency and community stability. *Amer. Zool.* 10: 17 - 25.
- Louw, W.J., 1976. Mesoclimate of the Port Elizabeth-Uitenhage metropolitan area. Pretoria Weather Bureau Technical Paper No. 4. Government Printer, Pretoria.
- Lubchenco, J., 1978. Plant species diversity in marine intertidal community: importance of herbivore food preference and algal competitive abilities. *Amer. Natur.* 112: 23 - 29.
- Maarel, E. van der, 1971. Plant species diversity in relation to management. In: E. Duffey & A.S. Watt (eds.), *The scientific management of animal and plant communities*, p. 45 - 63. Blackwell, London.
- Marchant, N.G., 1973. Species diversity in the south western flora. *J. Roy. Soc. Western Australia* 56: 23 - 30.
- Margalef, R., 1963. On certain unifying concepts in ecology. *Amer. Natur.* 97: 357 - 374.
- MacArthur, R.H., 1972. *Geographical ecology: patterns in the distribution of species*. Harper & Row, New York, 269 pp.
- MacArthur, R.H. & Wilson, E.O., 1967. *The theory of island biogeography*. Princeton University Press, Princeton, N.J., 203 pp.
- MacArthur, R.H., Diamond, J.M. & Karr, J.R., 1972. Density compensation in island faunas. *Ecology* 53: 330 - 342.
- McKenzie, B., 1978. A quantitative and qualitative study of the indigenous forests of the south-western Cape. Unpublished thesis, University of Cape Town.
- McKenzie, B., Moll, E.J. & Campbell, B.M., 1977. A phytosociological study of Orange Kloof, Table Mountain, South Africa. *Vegetatio* 34: 41 - 53.
- McNaughton, S.J., 1967. Relationships amongst functional properties of Californian grassland. *Nature* 216: 168 - 169.
- Moll, E.J. & White, F., 1978. The Indian Ocean Coastal Belt. In: M.J.A. Werger (ed.), *Biogeography and ecology of southern Africa*, p. 561 - 598. Junk, The Hague.
- Monk, C.D., 1967. Tree species diversity in the eastern deciduous forest with particular reference to north central Florida. *Amer. Natur.* 101: 173 - 187.
- Naveh, Z. & Whittaker, R.H., 1979. Structural and floristic diversity of shrublands and woodlands in northern Israel and other mediterranean areas. *Vegetatio* 41: 171 - 190.
- Newman, E.I., 1973. Competition and diversity in herbaceous vegetation. *Nature* 244: 310.

- Nicholson, S.A. & Monk, C.D., 1974. Plant species diversity in old field succession on the Georgia Piedmont. *Ecology* 55: 1075 - 1085.
- Nilsson, S.G. & Nilsson, I.N., 1978. Species richness and dispersal of vascular plants to islands in Lake Möckeln, southern Sweden. *Ecology* 59: 473 - 482.
- Odum, E.P., 1969. The strategy of ecosystem development. *Science* 164: 267 - 270.
- Olsvig, L., 1979. Pattern and diversity analysis of the irradiated oak-pine forest, Brookhaven, New York. *Vegetatio* 40: 65 - 78.
- Orians, G.H., 1975. Diversity, stability and maturity in natural ecosystems. In: W.H. van Dobben & R.H. Lowe-McConnel (eds.), *Unifying concepts in ecology*, p. 139 - 150. Junk, the Hague.
- Peet, R.K., 1974. The measurement of species diversity. *Ann. Rev. Ecol. Syst.* 5: 285 - 307.
- Peet, R.K., 1978. Forest vegetation of the Colorado Front Range: patterns of species diversity. *Vegetatio* 37: 65 - 78.
- Pianka, E.R., 1966. Latitudinal gradients of species diversity: a review of concepts. *Amer. Natur.* 100: 33 - 46.
- Pierce, S.M. & Cowling, R.M., 1982. Phenology of fynbos and non-fynbos communities in the south eastern Cape, South Africa. Unpublished ms.
- Reiners, W.A., Worler, I.A. & Lawrence, D.B., 1971. Plant diversity in a chronosequence at Glacier Bay, Alaska. *Ecology* 52: 55 - 69.
- Rice, B. & Westoby, M., 1982a. Plant species richness at tenth-hectare scale in Australian vegetation compared to other continents. Submitted to *Vegetatio*.
- Rice, B. & Westoby, M., 1982b. Species richness in vascular vegetation of the West Head, N.S.W. Submitted to *Austr. J. Ecol.*
- Richardson, P.J. & Lum, K., 1980. Patterns of plant species diversity in California: relation to weather and topography. *Amer. Natur.* 116: 504 - 536.
- Ricklefs, R.E., 1977. Environmental heterogeneity and plant species diversity: a hypothesis. *Amer. Natur.* 111: 376 - 381.
- Risser, P.G. & Rice, E.L., 1971. Diversity in tree species in Oklahoma upland forests. *Ecology* 52: 876 - 880.
- Roberts, B.R., Anderson, E.R. & Fourie, J.H., 1975. Evaluation of natural pastures: quantitative criteria for assessing conditions in the Themeda veld of the Orange Free State. *Proc. Grassld. Soc. sth. Afr.* 10: 133 - 140.
- Roux, P.W., 1966. Die uitwerking van seisoenreënval en beweiding op gemengde karooveld. *Proc. Grassld. Soc. sth. Afr.* 1: 103 - 110.
- Schulze, B.R., 1965. Climate of South Africa. Part 8. General survey. South African Weather Bureau 28. Government Printer, Pretoria, 330 pp.
- Schulze, R.E., 1975. Incoming radiation on sloping terrain: a general model for use in southern Africa. *Agrochimophysika* 7: 55 - 61.

- Schulze, R.E. & McGee, O.S., 1978. Climatic indices and classification in relation to biogeography of southern Africa. In: M.J.A. Werger (ed.), *Biogeography and ecology of southern Africa*, p. 19 - 52. Junk, The Hague.
- Shafi, M.I. & Yarranton, G.A., 1973. Diversity, floristic richness and species evenness during a secondary (post-fire) succession. *Ecology* 54: 879 - 902.
- Shmida, A. & Whittaker, R.H., 1979. Convergent evolution of deserts in the old and new worlds. In: O. Wilmanns & R. Tuxen (eds.), *Werden und Vergehen von Pflanzengesellschaften*, p. 437 - 450. J. Cramer, Vaduz.
- Sieb, R.L., 1980. Baja California: a peninsula for rodents but not for reptiles. *Amer. Natur.* 115: 613-620.
- Simpson, B.B., 1974. Glacial migrations of plants: island biogeographical evidence. *Science* 185: 698 - 700.
- Slatyer, R.O. (ed.), 1976. *Dynamic changes in terrestrial ecosystems: patterns of change, techniques for study and applications to management*. M.A.B. Technical Notes No. 4. UNESCO, Paris.
- Specht, R.L., 1979. Heathland and related shrublands of the world. In: R.L. Specht (ed.), *Heathlands and related shrublands of the world. A. Descriptive studies*, p. 1 - 18. Elsevier, Amsterdam.
- Specht, R.L. & Moll, E.J., 1982. Heathlands and sclerophyllous shrublands - an overview. In: F.J. Kruger, D.T. Mitchell and J.U.M. Jarvis (eds.), *Mediterranean-type ecosystems. The role of nutrients*. Springer, Berlin, Heidelberg, New York (in press).
- Taylor, H.C., 1978. Capensis. In: M.J.A. Werger (ed.), *Biogeography and ecology of southern Africa*, p. 171 - 229. Junk, The Hague.
- Taylor, R.J. & Regal, P.J., 1978. The peninsula effect on species diversity and the biogeography of Baja, California. *Amer. Natur.* 112: 583 - 593.
- Terborgh, J., 1973. On the notion of favourableness in plant ecology. *Amer. Natur.* 107: 481 - 501.
- Van der Merwe, C.V., 1976. *Die plantekologiese aspekte en bestuursprobleme van die Goukamma-Natuurreservaat*. Unpublished thesis, University of Stellenbosch.
- Van der Merwe, C.V., 1977. *'n Plantegroei opname van die De Hoop Natuurreservaat*. Bontebok 1: 1 - 29.
- Van Wilgen, B., 1980. *Some effects of fire frequency on fynbos at Jonkershoek, Stellenbosch*. Unpublished thesis, University of Cape Town.
- Vuilleumier, F. & Simberloff, D., 1980. Ecology versus history as determinants of patchy and insular distribution in high Andean birds. *Evol. Biol.* 13: 235 - 379.
- Weaver, M. & Kellman, M., 1981. The effects of forest fragmentation on woodlot tree biotas in Southern Ontario. *J. Biogeogr.* 8: 199 - 210.
- Werger, M.J.A., 1972. Species-area relationships and plot size: with some examples from South African vegetation. *Bothalia* 10: 583 - 594.
- Werger, M.J.A., 1978. Biogeographical division of southern Africa. In: M.J.A. Werger (ed.), *Biogeography and ecology of southern Africa*, p. 145 - 170. Junk, The Hague.

- Werger, M.J.A., Kruger, F.J. & Taylor, H.C., 1972. A phytosociological survey of Cape fynbos and other vegetation at Jonkershoek, Stellenbosch. *Bothalia* 10: 599 - 614.
- Westman, W.E., 1975a. Edaphic climax pattern of the pygmy forest region of California. *Ecol. Monogr.* 22: 1 - 44.
- Westman, W.E., 1975b. Pattern and diversity in swamp and dune vegetation, North Stradbroke Island. *Austr. J. Bot.* 23: 339 - 354.
- Westman, W.E., 1981. Diversity relations and succession in Californian coastal sage scrub. *Ecology* 62: 170 - 184.
- Westman, W.E., 1982. Spatial partitioning of resources. In: F.J. Kruger, D.T. Mitchell & J.U.M. Jarvis (eds.), *Mediterranean-type ecosystems. The role of nutrients* (in press).
- White, F., 1978. The Afromontane Region. In: M.J.A. Werger (ed.), *Biogeography and ecology of southern Africa*, p. 463 - 513. Junk, The Hague.
- Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* 30: 279 - 338.
- Whittaker, R.H., 1969. Evolution of diversity in plant communities. *Brookhaven Symp. Biol.* 22: 178 - 196.
- Whittaker, R.H., 1972. Evolution and measurement of species diversity. *Taxon* 21: 213 - 251.
- Whittaker, R.H., 1973. Direct gradient analysis: techniques and results. In: R.H. Whittaker (ed.), *Ordination and classification of communities*, p. 7 - 51. Junk, The Hague.
- Whittaker, R.H., 1975. The design and stability of plant communities. In: W.H. van Dobben & R.H. Lowe-McConnell (eds.), *Unifying concepts in ecology*, p. 169 - 181. Junk, The Hague.
- Whittaker, R.H., 1977. Evolution of species diversity in land communities. *Evol. Biol.* 10: 1 - 67.
- Whittaker, R.H. & Levin, S.A., 1977. The role of mosaic phenomena in natural communities. *Theor. Pop. Biol.* 12: 117 - 139.
- Whittaker, R.H. & Niering, W.A., 1965. Vegetation of the Santa Catalina Mountains. II. A gradient analysis of the south slope. *Ecology* 46: 429 - 452.
- Whittaker, R.H. & Niering, W.A., 1968. Vegetation of the Santa Catalina Mountains, Arizona. IV. Limestone and acid soils. *J. Ecol.* 56: 523 - 544.
- Whittaker, R.H. & Niering, W.A., 1975. Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production and diversity along the elevation gradient. *Ecology* 56: 771 - 790.
- Whittaker, R.H., Niering, W.A. & Crisp, M.D., 1979. Structure, pattern and diversity of a mallee community in New South Wales. *Vegetatio* 39: 65 - 76.

- Willis, A.J., 1963. Braunton Burrows: the effects on the vegetation of the addition of mineral nutrients to dune sands. *J. Ecol.* 51: 353 - 374.
- Zeevalking, H.J. & Fresco, L.F.M., 1977. Rabbit grazing and species diversity in a dune area. *Vegetatio* 35: 193 - 196.

PAPER 4

A COMPARISON OF FYNBOS AND NON-FYNBOS COENOCLINES IN THE
LOWER GAMTOOS RIVER VALLEY, SOUTH EASTERN CAPE, SOUTH AFRICA

Abstract

Patterns in the relative importance of structural attributes and growth forms along fynbos and non-fynbos coenoclines were studied to test the hypothesis that there would be less structural variation in the former because the overriding influence of low levels of soil nutrients would be manifest in a great deal of structural convergence in fynbos. The coenoclines were ranged along identical environmental gradients of increasing altitude, rainfall and soil moisture and decreasing climatic variability. Results showed that along the entire fynbos coenocline vegetation was structurally a small-leaved sclerophyllous shrubland with a graminoid understorey and, usually, a large-leaved (proteoid) shrub overstorey. Fynbos structure was interpreted largely as a response to low levels of soil nutrients. Non-fynbos vegetation ranged from mixed succulent-sclerophyllous and spiny large-leaved thicket at lower altitudes to tall mesic forest at the upper end of the gradient. Non-fynbos structure was explained in terms of variations in soil moisture and climate. An analysis of the biogeographical affinities of sample floras at sites along the coenoclines showed that fynbos vegetation was dominated by taxa endemic to the Cape phytochorion, although phytochorological mixing was pronounced at the lower altitude sites. The level of local endemism in fynbos coenocline was relatively high; nearly all endemics were Cape fynbos taxa and their incidence increased with increasing altitude. These data indicate that fynbos vegetation has had a lengthy history in the south eastern Cape and that high altitude sites would have comprised a refuge for Cape taxa during unfavourable climatic periods. Non-fynbos vegetation ranged from dry subtropical Tongaland-Pondoland thicket with a strong Karoo-Namib component to temperate Afromontane Forest. Levels of endemism were lower than the fynbos coenocline and decreased with increasing altitude. The high number of karroid endemics found in both coenoclines at low altitudes suggests that karroid vegetation would have been more widespread in the past, probably during last glacial which was considerably drier than the present Holocene interglacial.

Contents	Page
Introduction	256
Methods	256
Data collection	256
Data analysis	258
The Gradient	262
Results and discussion	266
Growth forms and structural attributes	266
Phytochorological affinities and endemism	276
General discussion and conclusions	281
References	283

Introduction

The south eastern (S.E.) Cape is a meeting point for four African phytochoria (Goldblatt, 1978; Werger, 1978a; Gibbs Russel & Robinson, 1981) and provides exciting potential for the study of vegetation types of disparate biogeographical affinities, found under broadly similar climatic conditions. Because of the complex geological features of the lower Gamtoos River Valley ($33^{\circ}50'S$, $24^{\circ}55'E$) (Fig. 1), I was able to study along similar environmental gradients parallel community gradients or coenoclines (Whittaker, 1967) of Cape fynbos shrublands on shallow, sandy, infertile soils and non-fynbos vegetation (subtropical thicket, Afromontane forest) on deep, more fertile and heavier soils.

The aim of this study was to investigate for both coenoclines, parallel changes in growth forms, structural attributes, biogeographical affinities of the flora and patterns of endemism. Specifically the study was designed to test the hypothesis that the physiognomic-structural features of fynbos are determined largely by low levels of available nutrients (heathland syndrome of Specht, 1979; see also Cowling & Campbell, 1980) whereas the structure of non-fynbos vegetation on more fertile soils could be interpreted as a response to variations in soil moisture and climate. This hypothesis predicts that along a complex environmental gradient of increasing rainfall and decreasing temperature there would be less structural variation in fynbos than non-fynbos vegetation.

Methods

Data collection

Five matching sites were located in fynbos and non-fynbos vegetation at about 100 m intervals along parallel elevational gradients from approximately sea level to 500 m altitude, in the lower Gamtoos River Valley (Fig. 1). At each site four 100 m^2 plots were placed, by random walk, on different aspects (N, S, E and W) on open gentle slopes. The two uppermost non-fynbos sites were in colluvial basins with relatively steep sided walls and were more protected than the corresponding fynbos sites. Hereafter I refer to the parallel community gradients as the fynbos (FC) and non-fynbos (NFC) coenoclines.

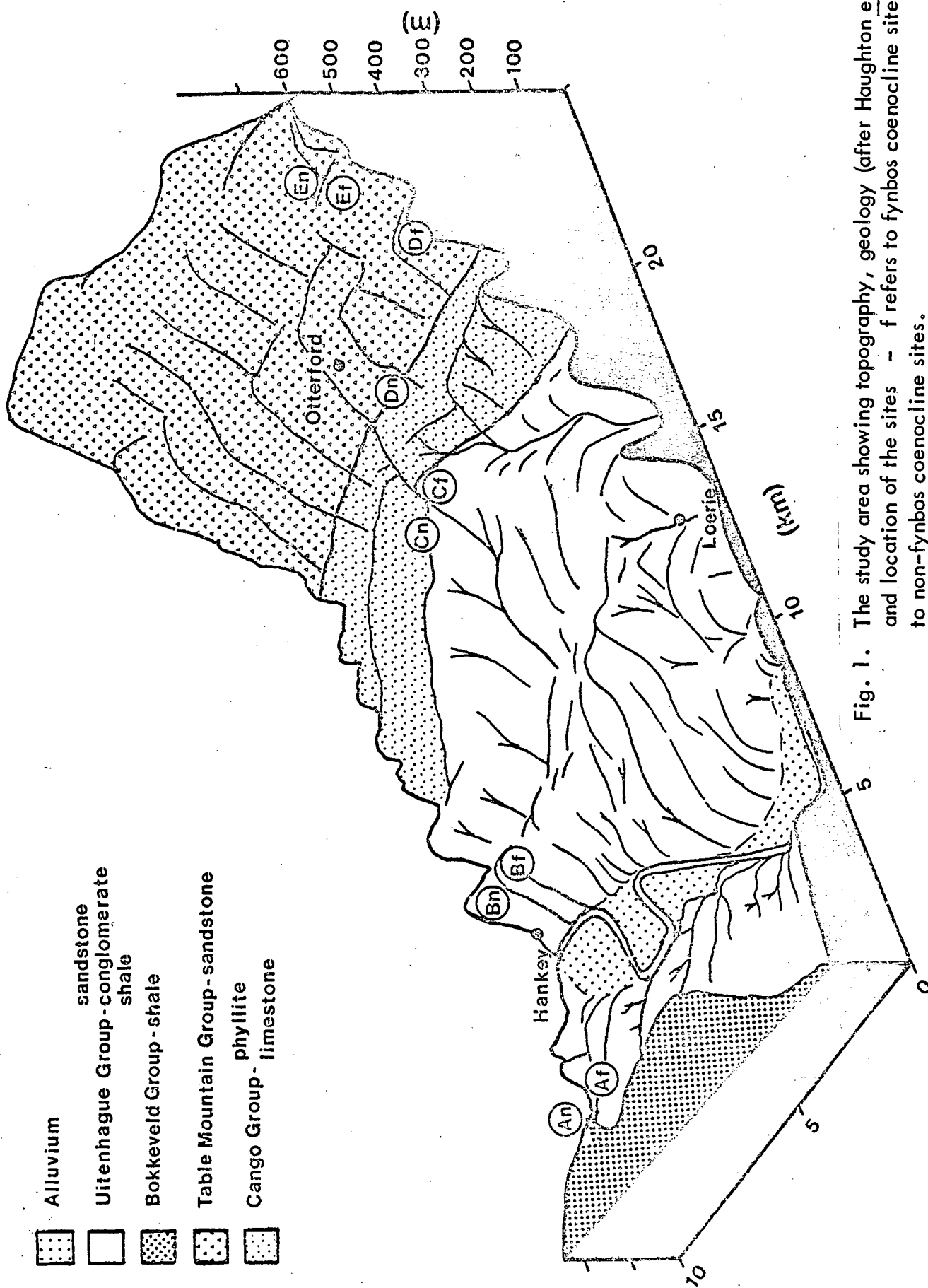


Fig. 1. The study area showing topography, geology (after Houghton et al., 1937) and location of the sites - f refers to fynbos coenocline sites, n refers to non-fynbos coenocline sites.

In each plot I subjectively estimated percentage projected canopy cover of each species. Species were classed into growth forms and additional structural data were recorded (Table 1). The physiognomic-structural attributes were easily observed or measured characters to which some functional or adaptive significance could be attributed (cf. Parsons, 1976; Bond, 1981). The definition of leaf texture categories, and their recognition in the field, remains problematic (Loveless, 1962; Small, 1973; Beadle, 1966; Bond, 1981). I used a subjective categorization of leaf texture by "feel" (Bond, 1981; Cowling & Campbell, 1982). Subsequent analyses of leaves subjectively classed as sclerophyll, orthophyll, fleshy (semi-succulent) and succulent showed real differences in leaf specific weight, thus lending credence to the "feel" method (Cowling & Campbell, 1982).

Site variables measured in each plot included soil depth and subjective estimates of litter and rock cover. At each site altitude was determined from 1: 50,000 topographic sheets and average annual rainfall from 1: 250,000 isohyet maps. Soils samples were collected at 15 cm depth from north and south aspect plots at corresponding sites on both coenoclines and analyzed for texture, pH and major nutrients by the Department of Agriculture and Fisheries soils laboratory in Stellenbosch. Soil data are shown in Table 2.

The vegetation at all sites was relatively undisturbed. All the fire-prone fynbos sites were unburnt for at least 12 yr and the non-fynbos sites for several decades or even centuries. Therefore within each coenocline, successional variations are unlikely to affect community structure.

Data analysis

Gradient analysis

Gradient analysis is a powerful technique which has led to significant advances in the understanding of vegetation structure and compositional change (Whittaker, 1967; 1973; Peet and Loucks, 1977). I used direct gradient analysis (Whittaker, 1967) to compare the variation in community structure of two coenoclines spanning similar climatic gradients but each having different soils. This technique, called coenocline comparisons (Whittaker, 1967), has been used to compare community gradients under similar climates on different parent materials (Whittaker, 1960; Whittaker & Niering, 1968), different

Table 1. Growth forms and structural attributes

Growth forms	Leaf texture (Cowling & Campbell, 1982)
Woody, evergreen	Sclerophyllous
Woody, deciduous	Orthophyllous
Herbaceous	Fleshy (semi-succulent)
Succulent	
Woody growth forms	Leaf size (Raunkiaer, 1934)
Subshrubs (< 0.25 m)	Leptophyll
Shrubs (0.25 - 5.0 m)	Nanophyll
Trees (5.0 - 10.0 m)	Microphyll
Tall trees (> 10.0 m)	Mesophyll
Herbaceous growth forms	Spinescence
Seasonal graminoids	Leafspines
Non-seasonal graminoids	Stemspines
Geophytes	
Non-geophytic forbs	
Climbers	

Table 2. Soil data for sites along the fynbos and non-fynbos coenoclines.
 N refers to a sample from a north slope, S from a south slope.
 Soil samples taken at 0.15 m depth.

Transect site		Texture ¹	% sand ²	pH ³	S value ⁴ (me %)	Oxidizable carbon ⁵ (%)	Total nitrogen ⁶ (%)	Available phosphorus ⁷ (ppm)
FYNBOS COENOCLINE								
A	N	Sandy loam	73.8	4.6	7.13	7.7	0.22	8
	S	Sandy loam	80.4	4.2	1.58	1.5	0.06	2
B	N	Loamy sand	87.0	4.8	2.31	1.7	0.06	2
	S	Sandy loam	80.9	4.7	3.54	2.2	0.10	3
C	N	Loamy sand	86.2	4.8	4.88	3.3	0.09	2
	S	Sandy loam	78.1	4.8	4.34	3.3	0.07	3
D	N	Sandy loam	77.0	4.0	3.7	7.5	0.07	3
	S	Loamy sand	85.0	3.9	1.3	2.6	0.15	6
E	N	Loamy sand	89.8	4.2	2.0	3.1	0.06	3
	S	Sandy loam	83.5	4.2	3.3	5.1	0.11	4
NON-FYNBOS COENOCLINE								
A	N	Loam	66.0	3.9	9.2	7.1	0.18	25
	S	Clay loam	40.0	5.2	16.5	6.5	0.29	10
B	N	Sandy clay loam	66.0	4.4	7.8	4.2	0.16	9
	S	Sandy loam	67.8	7.0	30.4	5.7	0.20	11
C	N	Loam	52.8	5.7	13.9	6.0	0.23	4
	S	Loam	55.0	6.5	27.1	22.1	0.43	10
D	N	Loam	67.0	4.5	8.8	10.4	0.39	25
	S	Sandy loam	71.0	3.6	4.4	8.2	0.20	11
	N	Sandy loam	69.8	3.1	3.1	12.8	0.60	14
	S	Loam	61.8	3.6	8.9	12.7	0.42	8

- 1 Textural classes according to MacVicar *et al.* (1977).
- 2 Pipette method.
- 3 1 N KCl 1 : 2.5 soln.
- 4 Sum of exchangeable cations. 1 N NH₄ acetate.
- 5 Walkley-Black method.
- 6 Kjeldahl.
- 7 Bray No. 2 (acid extraction, pH 3).

landscapes (Bond 1981) and different continents (Parsons & Moldenke, 1975; Cowling & Campbell, 1980).

At each site I averaged for the four plots the importance of the structural and biogeographic measures and plotted these averages along an elevational gradient to discern parallel trends in both coenoclines. I also used a reciprocal averaging (RA : Hill, 1973) ordination of both coenoclines to check whether the compositional gradients thus derived, mirrored the elevational gradient.

Phytochorological affinities and endemism

I determined the phytochorological affinity of each species according to their distribution in relation to established phytochoria (Werger, 1978a). The distribution of taxa were established from locality records in the Albany Museum Herbarium (GRA) and the Bolus Herbarium (BOL) and also from relevant taxonomic revisions. Species were classified as follows:

- (i) endemic to a particular phytochorion;
- (ii) linking two (usually) adjacent phytochoria;
- (iii) widely distributed, common to tropical and subtropical phytochoria;
- (iv) widely distributed, occurring in temperate and tropical phytochoria and often having extra-African distributions.

Categories (ii) – (iv) are ecological and chorological transgressor species (White, 1978). Details on the distribution tracks and examples of species distributions are given in Cowling (1982a). A list showing the classification of species into phytochorological groups is available on request.

For each plot I determined an index of phytochorological diversity (PD) using the Shannon-Wiener function where

$$PD = - \sum p_i \log p_i$$

in which p_i is the number of species in phytochorological group i expressed as a fraction of the total number of species in the plot.

The number of species endemic to the S.E. Cape was determined for each plot. These included species of Cape affinity restricted to Weimarck's (1941) South Eastern Centre

of the Cape Region, and subtropical, karroid and Afromontane endems confined to the Kaffrarian Transition Zone (Cowling, 1982a).

The Gradient

Both coenoclines were ranged along an altitudinal gradient. Altitude is not a variable directly influencing vegetation but an index for a variety of climatic factors which affect site moisture and nutrient status. Aspect and terrain slope have an important bearing on radiant energy regimes which, in turn, lead to corresponding variation in soil moisture status (Holland & Steyn, 1975; Granger & Schulze, 1977) and pedogenesis (Garland, 1979; Bond, 1981). At 36°S north slopes of 10° receive about twice as much energy as equivalent south slopes in midwinter, and about 1.5 times as much at the equinoxes (Schulze, 1975). On both coenoclines all plots were on gentle to moderate slopes (8° - 16°) and located on different aspects at each site. Thus the average importance of a particular structural attribute at each site reflects the full range of radiant energy regimes at that site.

Climate diagrams from two stations along the gradient are shown in Fig. 2. The extremes of the gradient represent two distinct climates. Hankey has a climate typical of coastal plain valley bottoms in the S.E. Cape. Temperatures are higher than adjacent coastal mountain and maritime areas. The valley bottom also has the highest absolute maximum (40°C) and lowest minimum (-1.1°C) and greatest diurnal temperature variation throughout the year (cf. Louw, 1976). Valley areas receive considerably less precipitation than mountains where rainfall is under stronger orographic control. Rainfall is highly variable from year to year and may fall in any month although long term averages indicate spring and autumn maxima (Fig. 2).

Otterford, the upper station (Fig. 2), typifies the coastal mountain climate which is cooler, wetter and less variable than the valley. Cool marine air keeps the temperatures equable throughout the year although frost and snow are occasional in winter. Precipitation is high (900 mm yr⁻¹) and rain may fall in every month of the year with peaks in spring and autumn.

There are fundamental differences between the soils of both coenoclines. FC soils are shallower, rockier, sandier and less fertile than NFC soils at corresponding sites (Table 2). FC soils are rocky, sandy lithosols derived from conglomerates and sandstones of the Uitenhage Group at sites A - C, and from Table Mountain Group sandstones at sites

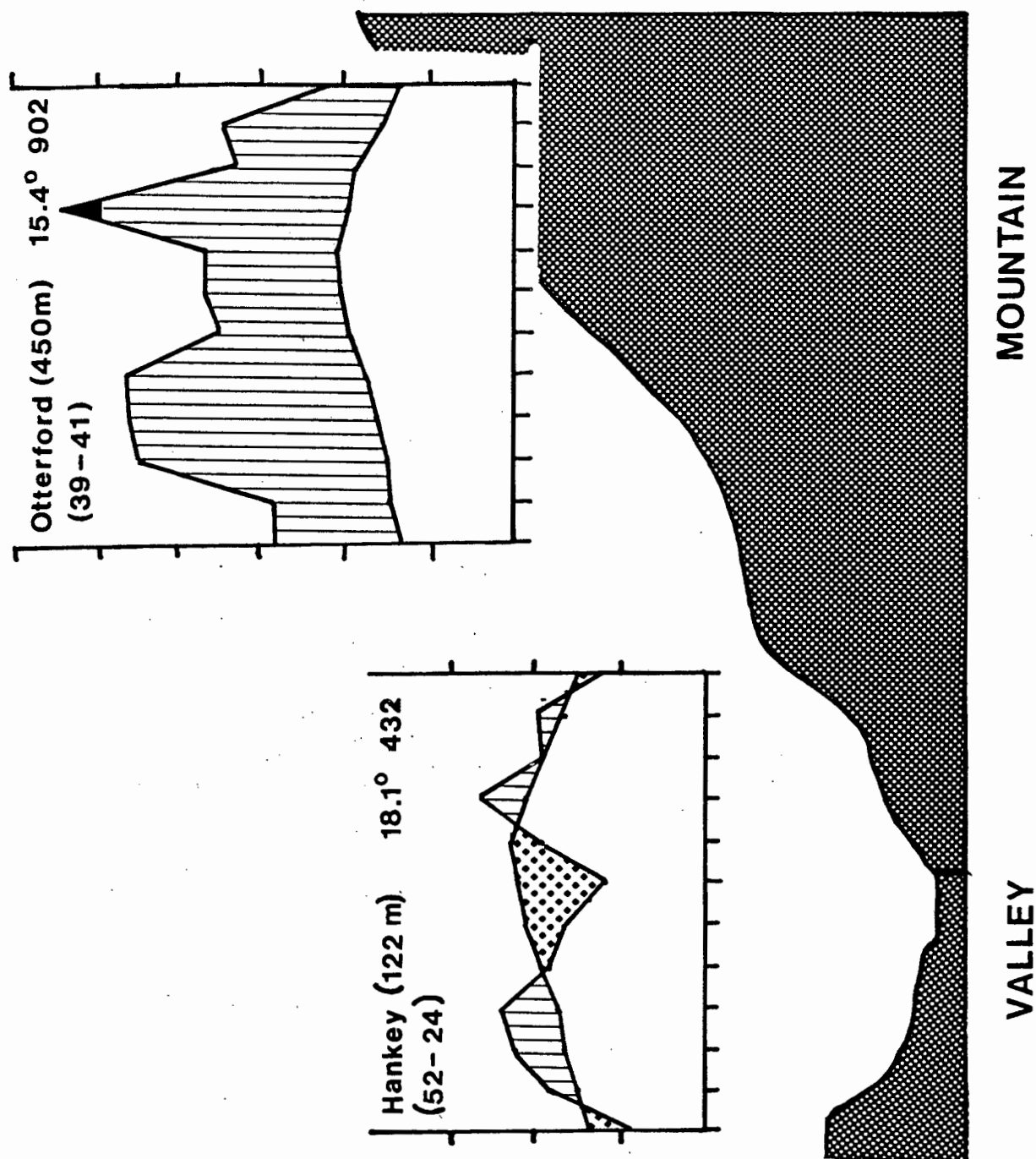


Fig. 2. Climate diagrams (mean monthly air temperature and rainfall) for two stations along the Gamtoos transect. Temperature data adapted from climatically similar nearby stations (Uitenhage (108m, 52yr) for Hankey, Van Stadens (452m, 39 yr) for Otterford). Hankey is representative of sites A - B and Otterford of sites D - E.

D and E (Fig. 1). NFC soils are deep (≥ 1 m) non-rocky, loams derived from Bokkeveld Group shales at site A, Uitenhage Group mudstones at site B and Congo group limestones at site C; soils at sites D and E are very deep and of colluvial origin. NFC soils are not only more fertile than corresponding FC soils but also have superior water holding capacity as evinced by their greater depth and heavier texture (Brady, 1974).

Fig. 3 is a trace of the first-axis RA scores for the 20 plots of both coenoclines in their sequence along the altitudinal gradient from xeric north aspect plots at site A to mesic south aspect plots at site E. The trace is a faithful reflection of the location of sites along the altitudinal gradient. Particularly in the FC, north aspect plots tended to group closer to plots from sites immediately below them on the gradient, than with plots on other aspects from the same site. The RA scores can be used to express the rates of compositional change along the transect (Whittaker *et al.*, 1979). The FC was indicative of a continuum whereas the NFC showed an important compositional discontinuity between sites C and D.

The primary RA axis of the FC data was significantly correlated with altitude ($r = -.92$; $p < .001$), rainfall ($r = -.90$, $p < .001$), soil pH ($r = .61$; $p < .05$) and sum of exchangeable bases ($r = -.61$; $p < .05$). The RA axis of the NFC data did not show linear relationships with environmental variables (Fig. 3). There were significant correlations with altitude ($r = -.91$; $p < .001$), rainfall ($r = -.90$; $p < .001$), percentage sand ($r = .52$; $p < .02$), soil pH ($r = .68$; $p < .05$), sum of exchangeable bases ($r = .59$; $p < .1$), total soil nitrogen ($r = -.64$; $p < .05$) and soil organic carbon ($r = .82$; $p < .01$). Soil chemical data for both coenoclines are from a subsample of 10 plots.

Both coenoclines are ranged along complex gradients (*sensu* Whittaker, 1960; 1967) of increasing altitude and rainfall and decreasing temperature and climatic variability. Soil moisture conditions are likely to improve with increasing altitude. Furthermore there is a tendency for base status and pH to decrease with increasing altitude, probably because of more precipitation, reduced evapotranspiration, lower temperatures and thus a more effective leaching of soils at the upper sites (Hanawalt & Whittaker, 1976).

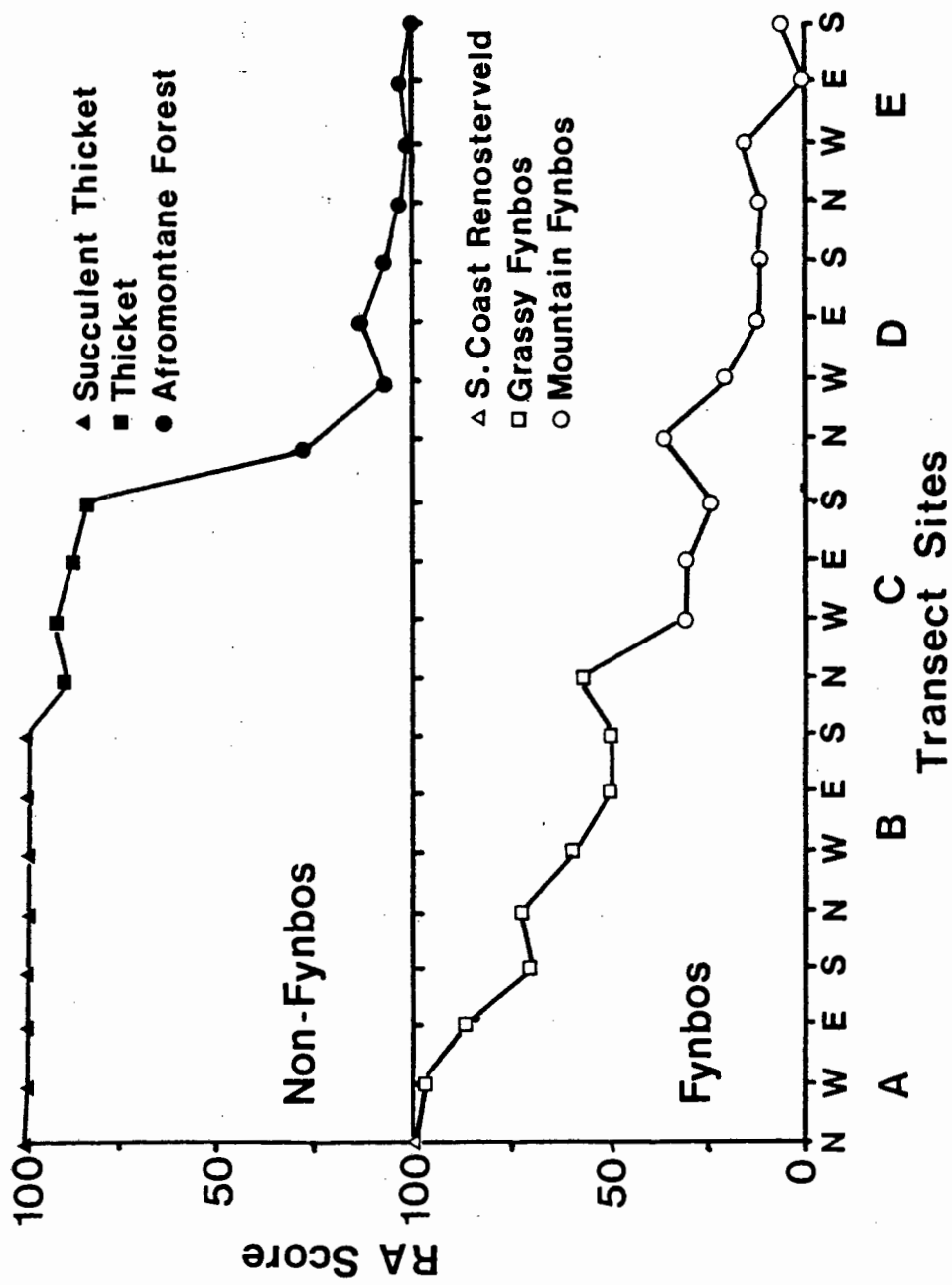


Fig. 3. Reciprocal averaging trace for the 20 plots of the fynbos and non-fynbos coenoclines. Plots are arranged from the xeric north aspect (N) at site A to the mesic south aspect (S) at site E.

In the NFC soil nitrogen and organic carbon, both highly interrelated variables, increased with increasing elevation, probably because of slower decomposition rates at the cooler, wetter, high altitude sites (Brady, 1974).

The vegetation of the study area and adjacent coastal plain has been classified hierarchically into a series of classes, orders and communities (Cowling, 1982b). Vegetation orders, structural characterization and dominant species at each site on both coenoclines are shown in Table 3 (see also Fig. 3). The marked compositional discontinuity between sites C and D of the NFC (Fig. 3) indicates a critical altitude (Richards, 1964) between subtropical thicket and Afromontane forest. Moll & White (1978) and Chapman & White (1970) have noted that the zone of demarcation between temperate Afromontane forests and tropical lowland communities is often abrupt in southern and east Africa respectively, whereas Hamilton (1975) describes a continuum in a Ugandan forest. In the S.E. Cape there is an intermingling of subtropical and Afromontane forest elements along the level coastal plain (see Acocks' (1953) Alexandria Forest veld type) but the pattern observed in the Gamtoos Valley is consistent with the general observation of a well defined zonation along steep environmental gradients (Beals, 1969).

Results and discussion

Growth forms and structural attributes

Growth forms

Fig. 4a shows the mean relative cover of woody evergreen, woody deciduous, herbaceous and succulent growth forms at sites along both coenoclines. Woody evergreen growth forms were overwhelmingly dominant in both the FC and the NFC. A high incidence of evergreenness is to be expected in fynbos vegetation growing on infertile soils where the cost of rebuilding deciduous photosynthetic organs may place too great a burden on the plant's nutritional resources (Monk, 1966; Small, 1972; Moore, 1980). There is a general correlation between soil fertility and leaf longevity, and both Australian heathlands and South African fynbos which are associated with impoverished soils, are dominated by evergreen species (Beadle, 1966; Johnson & Briggs, 1975; Specht, 1979; Cowling & Campbell, 1980; Bond, 1981).

Table 3. Vegetation data for sites along the fynbos and non-fynbos coenoclines

Transect site	Order ¹	Structural characterization ²	Dominant species
FYNBOS COENOCLINE			
A	South Coast Renosterveld/ Grassy Fynbos	Low Mid-dense Grassy Small-leaved Shrubland	<u>Elytropappus rhinocerotis</u> , <u>Themeda triandra</u> , <u>Erica demissa</u> , <u>Pentaschistis colorata</u>
B	Grassy Fynbos	Low Mid-dense Ericoid Shrubland with a Mid-high Mid-dense Proteoid Shrub Overstorey	<u>Protea neriifolia</u> , <u>Muraltia squarrosa</u> , <u>Restio triticeus</u> , <u>Trachypogon spicatus</u>
C	South Eastern Mountain Fynbos/Grassy Fynbos	Low Mid-dense Heathland with a Mid-high Mid-dense Proteoid Shrub Overstorey	<u>Protea neriifolia</u> , <u>Leucadendron eucalyptifolium</u> , <u>Hypodiscus alboaristatus</u> , <u>Tetraria compressa</u>
D	South Eastern Mountain Fynbos	Mid-high Mid-dense Proteoid Shrubland with a Low Open Heath Understorey	<u>Leucadendron eucalyptifolium</u> , <u>Thamnus multiflorus</u> , <u>Hypodiscus alboaristatus</u> , <u>H. striatus</u>
E	South Eastern Mountain Fynbos	Closed Restioland with a Tall Mid-dense Proteoid Shrub Overstorey	<u>Leucadendron loerinse</u> , <u>Erica copiosa</u> , <u>Hypodiscus synchroolepis</u> , <u>H. striatus</u>
NON-FYNBOS COENOCLINE			
A	Kaffrarian Succulent Thicket	Mid-high Closed Large-leaved and Succulent Shrubland	<u>Euclea undulata</u> , <u>Portulacaria afra</u> , <u>Pappea capensis</u> , <u>Putterlickia pyracantha</u>
B	Kaffrarian Succulent Thicket	Tall Closed Large-leaved and Succulent Shrubland with a Sparse Low Succulent Tree Overstorey	<u>Euclea undulata</u> , <u>Sideroxylon inerme</u> , <u>Aloe ferox</u> , <u>Hypoestes verticillaris</u>
C	Kaffrarian Thicket	Tall Closed Large-leaved Shrubland	<u>Sideroxylon inerme</u> , <u>Ochna serrulata</u> , <u>Euclea undulata</u> , <u>Olea europaea</u>
D	Afromontane Forest	Low Forest with a Tall Mid-dense Tree Overstorey	<u>Gonioma kamassi</u> , <u>Brachylaena glabra</u> , <u>Rapanea melanophloeos</u> , <u>Podocarpus falcatus</u>
E	Afromontane Forest	Tall Forest	<u>Gonioma kamassi</u> , <u>Ocotea bullata</u> , <u>Olea capensis</u> ssp. <u>macrocarpa</u> , <u>Curtisia dentata</u>

¹ Order concept according to Cowling (1982b)² Structural characterization according to Campbell et al. (1981)

The nutritional hypothesis does not explain the evergreenness of NFC sites. At lower altitudes I explain the advantages of evergreenness in terms of the plant's capacity for opportunistic growth, whenever conditions are suitable (Mooney & Dunn, 1970; Morrow & Mooney, 1974; Miller, 1982). By holding onto its leaves the plant is able to solve the problem of unpredictable rains at lower altitudes. Furthermore soils are deep and so are the rooting systems of the evergreen shrubs; even during dry periods some moisture probably remains in the profile and limited photosynthetic activity occurs (cf. Mooney *et al.*, 1975). Pierce & Cowling (1982) have shown that in the study area evergreen thicket shrubs are capable of growing at any time of the year. At the higher altitude NFC sites water is probably never limiting and temperatures are equable: evergreenness is favoured.

Herbaceous growth forms had a higher cover at all FC sites compared to corresponding NFC sites (Fig. 4a). Bond (1981) interprets fynbos structure in terms of a savanna model where, depending on rainfall and soil properties, a balance is maintained between graminoids (dominant herbs in fynbos; see Fig. 5c) utilizing surface moisture and shrubs utilizing deeper moisture reserves (Walter, 1979). The cover of herbaceous growth forms along the FC was consistent with Bond's (1981) predictions. All soils along the transect are shallow and stony which limits the soil storage capacity and thus the moisture available for the deeper rooted woody elements: hence the relatively high herbaceous cover. At the mesic end of the gradient the expected higher cover of deeper rooted shrubs due to more favourable soil moisture conditions, is offset by the extremely shallow soils there. Highest cover of woody species was found at site B which had the deepest soils (cf. Bond, 1981). The NFC communities are all closed shrublands or forests and all sites had similar cover of shade-tolerant herbs. (Fig. 4a).

Where annual precipitation is low the storage of water by plants represents an ecological adaptation; the plant is able to overcome periods of water deficiency with endogenous water reserves. It would be desirable, though not possible in this study, to correlate succulence with crassulacean acid metabolism (CAM) mode of carbon gain. A high degree of succulence is, in itself, not a criterion for CAM; only those succulents which unify the sites of malic acid synthesis, storage and conversion within the same cells, can be expected to have CAM (Kluge & Ting, 1978). In our study area most of the predominant succulent genera (Euphorbia, Crassula, Portulacaria, Delosperma, Aloe, Senecio) are known to possess CAM (Mooney *et al.*, 1977) while another (Zygophyllum) is non-CAM (Kluge & Ting, 1978).

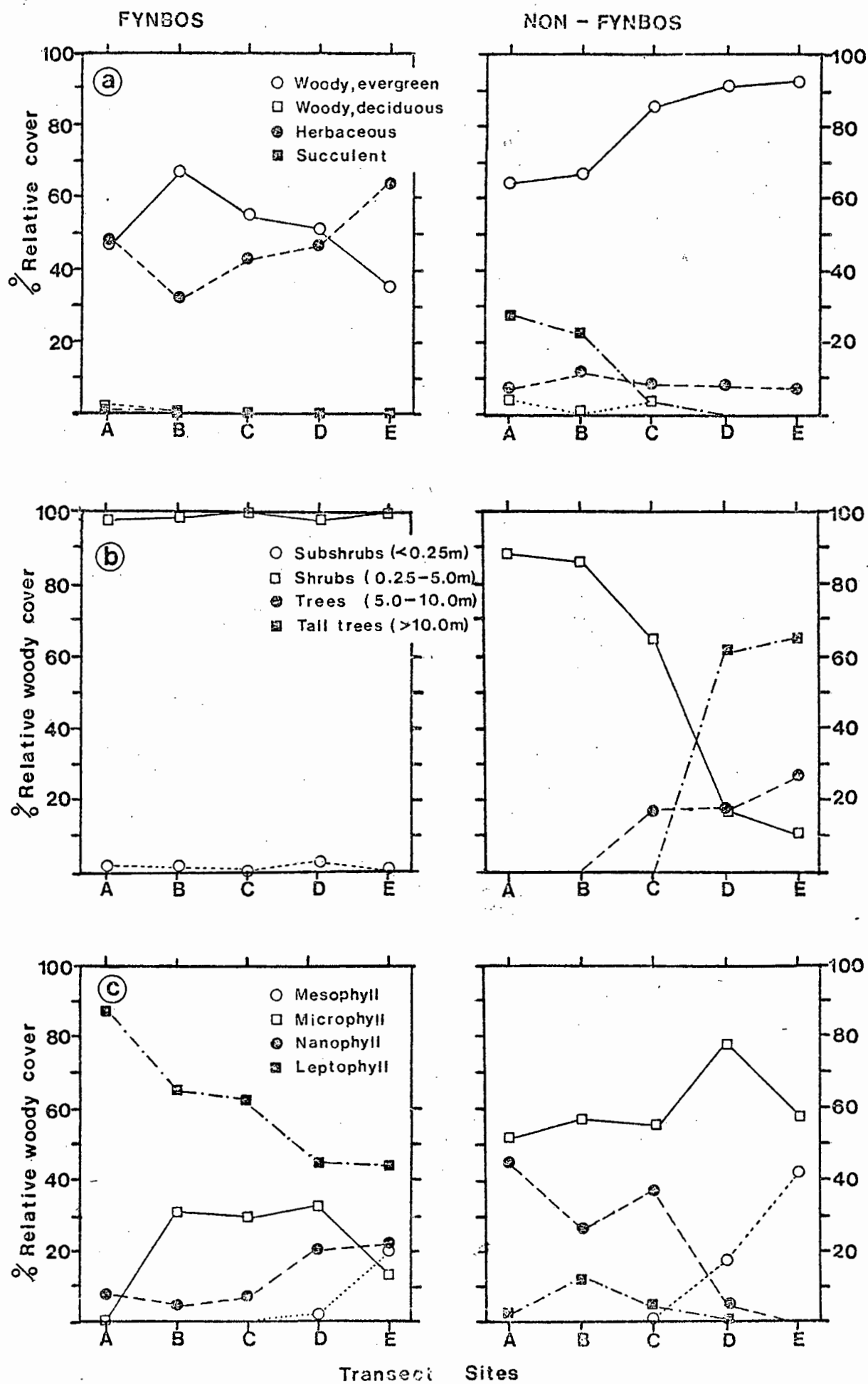


Fig. 4. Relative importance of a) growth forms, b) woody growth forms, and c) leaf size categories in the fynbos and non-fynbos coenoclines.

CAM succulents are extremely economical in terms of the ratio of carbon gained to water lost but have associated costs of low rates of carbon fixation and are not competitive where soil moisture is not limiting for extended periods (Kluge & Ting, 1978).

Predictably succulents had maximum cover in the low altitude valley climate areas (Fig. 4a) with low and unpredictable rainfall and great temperature fluctuations. It has been shown that optimal growth of some CAM species occurs under conditions of low night ($10^{\circ} - 15^{\circ}\text{C}$) and high day ($25^{\circ} - 30^{\circ}\text{C}$) temperatures (Kluge & Ting, 1978).

Succulents were virtually absent from the FC where they were largely replaced by fleshy (semi-succulent) leaved shrubs (Fig. 5a, see above). They were particularly common at NFC sites A and B. Succulents are shallow rooted drought endurers capable of opportunistic growth whenever there is moisture in the upper soil profile. In the drier sites they coexist with deeper rooted evergreen shrubs. It is tempting to speculate that in the S.E. Cape succulents replace the shallow rooted graminoids of the subtropical and tropical summer rainfall valley thickets (see Acocks, 1953; Edwards, 1967).

Woody growth forms

Fig. 4b shows the mean importance, expressed as a percentage, of the woody cover, of subshrubs, shrubs, trees and tall trees at sites along both coenoclines. The FC sites were dominated by shrubs throughout the gradient and there was no tendency for vegetation height to show any relationship with altitude (cf. Rutherford, 1978). Along the NFC shrub importance declined and tree importance increased with increasing altitude. Overall structure ranged from mid-high shrublands at site A to tall forests at site E (Table 3).

It has been stated that the scarcity of trees in fynbos is due to fire history (Moll *et al.*, 1980). A more plausible argument is that unlike Australia, the South African tree flora appears to have no ectotrophic mycorrhiza and is thus unable to colonize the infertile fynbos soils (Bond, 1981).

Leaf size

Leaves are plant organs which show clear adaptations to varying conditions of temperature, light, water and nutrients. Leaves have been the subject of many optimization models (Gates, 1968; Parkhurst & Loucks, 1972; Taylor, 1975; Givinish & Vermeij, 1976; Orians & Solbrig, 1977). Because of the assumed and proven adaptive significance of leaf characters, they have often been used as attributes for structural classifications of floristically complex vegetation (Webb, 1959; Grubb *et al.*, 1963; Bond, 1981; Campbell, 1982).

Small leaves are able to regulate leaf temperature and transpiration rate more efficiently than larger leaves. Because of this greater capacity for convective heat dissipation, small leaves are able to avoid lethal temperatures and minimize the amount of water transpired per CO₂ fixed. Irrespective of their assumptions, most models predict that small leaves should predominate in xerothermic environments (Gates, 1968; Parkhurst & Loucks, 1972; Taylor, 1975). There is much empirical evidence to support this prediction (Parsons & Moldenke, 1975; Werger & Ellenbroek, 1978; Hamman, 1979; Mooney *et al.*, 1974; Mooney *et al.*, 1978).

Small leaves are also associated with infertile soils (Loveless, 1962; Beadle, 1966; 1968; Givinish & Vermeij, 1976). Lower levels of nutrients limit photosynthetic rates (Mooney, 1982) and therefore decrease the ratio of CO₂ assimilated to water lost, thus providing a selective force for small leaves which minimize transpirational losses (Givinish & Vermeij, 1976).

The trend in leaf size patterns along the NFC conformed to heat budget predictions (Fig. 4c). There was a general decline in leptophyll-nanophyll and an increase in microphyll-mesophyll leaf sizes with increasing altitude, although microphylls predominated throughout the gradient. Patterns along the FC were largely consistent with the nutrient hypothesis (cf. Specht, 1979; Cowling & Campbell, 1980). Leptophylls dominated at all sites along the gradient but the tendency for large leaves to increase in importance at the highly infertile upper sites is unexplained by the nutrient hypothesis. Bond (1981) and Goble-Garrat *et al.* (1981) found limited support for heat budget and soil moisture effects on leaf size patterns in South African and Western Australian heathlands respectively.

Leaf texture

Leaf texture has long been cited as a structural feature which correlates well with regional climatic regime (e.g. Schimper, 1903). The adaptive significance of leaf texture has been the focus of a number of studies (Ferri, 1961; Loveless, 1962; Beadle, 1966; 1968; Small, 1972; 1973; Mooney *et al.*, 1975; Morrow & Mooney, 1974; Orians & Solbrig, 1977; Camerik & Werger, 1980) while leaf texture *per se* is used as an attribute for structural classifications with purely phytosociological objectives (Webb, 1959; Bond, 1981; Campbell, 1982). Patterns in the importance of different leaf texture categories along both coenoclines of the Gamtoos gradient have been dealt with elsewhere (Cowling & Campbell, 1982). I will briefly review these results below.

Fleshy or semi-succulent leaves were most common at the xeric end of the FC (see also Bond, 1981) (Fig. 5a) but were uncommon at corresponding non-fynbos sites where they were replaced by succulents (Fig. 4a). As yet, the water relations and carbon gaining mechanisms of evergreen, fleshy-leaved plants have not been studied.

There are two major hypotheses to explain the relative fitness of sclerophyll leaves to a particular habitat. The "drought" hypothesis, originally stated by Schimper (1903) is best articulated by Orians & Solbrig (1977). Sclerophylly has also been interpreted as a response to low levels of soil nutrients, particularly phosphorus and nitrogen (e.g. Loveless, 1962).

Orians & Solbrig (1977) have developed a descriptive cost-income model which takes into account water loss and carbon gain as well as morphological and physiological traits that affect these processes. Sclerophyllous leaves are interpreted as "high cost - slow profit" structures which are able to withstand high negative leaf water potentials through the development of energetically expensive supporting structures (Mooney & Dunn, 1970; Harrison *et al.*, 1971; Morrow & Mooney, 1974). These and other biochemical changes restrict high photosynthetic rates when water is available but allow the plant to yield profits when more mesophytic leaves have become an energetic liability (Mooney & Dunn, 1970; Morrow & Mooney, 1974; Mooney *et al.*, 1975). Sclerophyll leaves are mostly longlived.

Orthophyllous leaves ("low cost - quick profit") are cheaper to build and maintain per unit surface area and yield profits at faster rates than sclerophyllous leaves, provided soil water potential is low (Harrison *et al.*, 1971). As negative soil water potential builds up, they cease to yield profits but maintenance costs continue, resulting in a

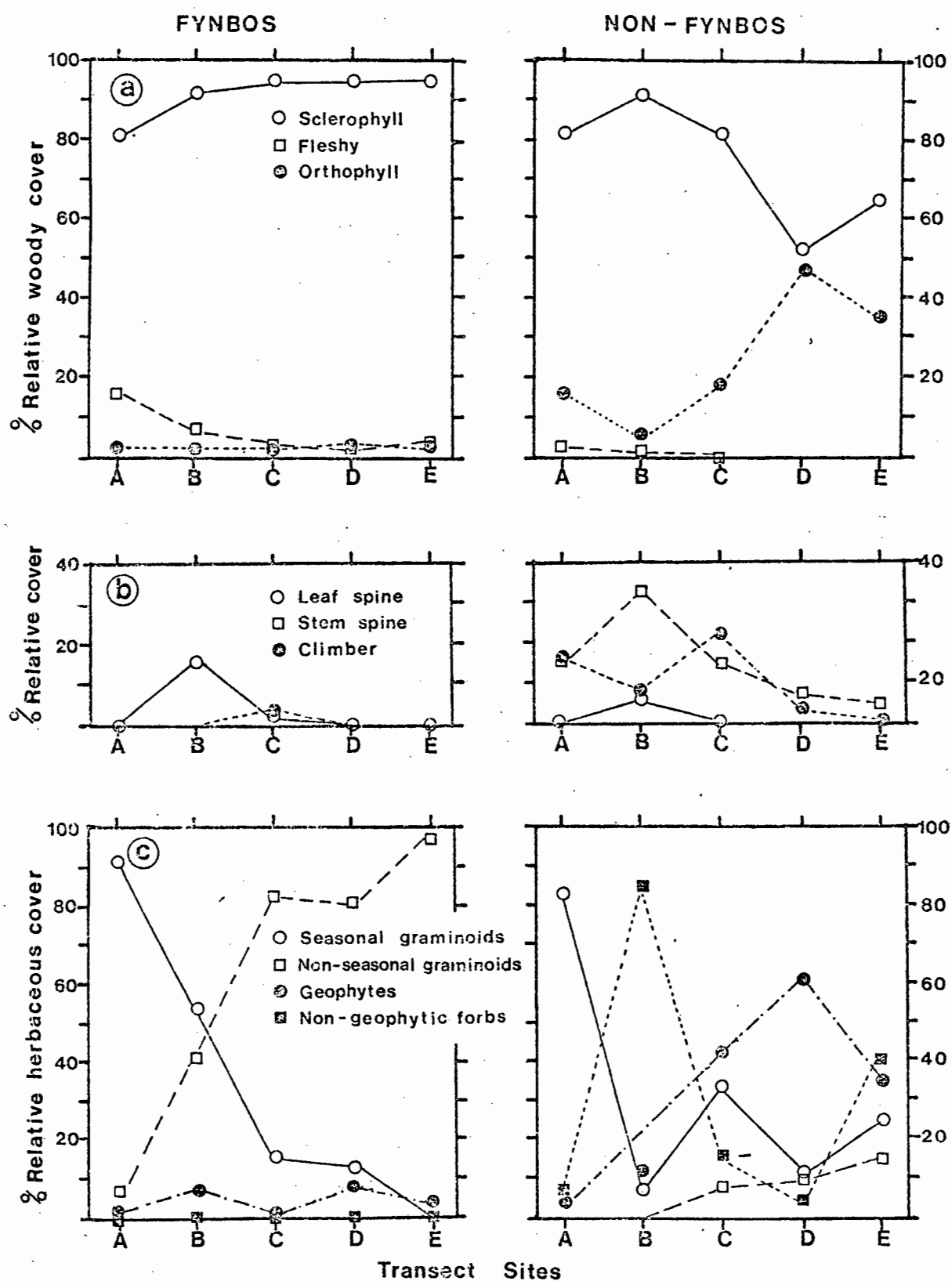


Fig. 5. Relative importance of a) leaf texture categories, b) spines and climbers, and c) herbaceous growth forms in the fynbos and non-fynbos coenoclines.

net loss in keeping the leaf (Orians & Solbrig, 1977). It is clearly beneficial to drop leaves under these conditions.

This model predicts that sclerophyll leaves are at a competitive advantage where periods of adequate soil moisture availability are short and erratic during the growing season (e.g. semi-desert) or in mesothermic mediterranean climates where deep rooted species can maintain net assimilation, although low at times, throughout the dry summer (Mooney & Dunn, 1970). Orthophyll leaves will be favoured in tropical savanna, tropical rain forest and temperate broadleaf forest climates (Orians & Solbrig, 1977).

In recent years evidence has accumulated to support the hypothesis that a sclerophyllous leaf is the expression of a metabolism found in plants that can tolerate low levels of certain nutrients, particularly phosphorus (Arens, 1958; Ferri, 1961; Loveless, 1962; Beadle, 1966; 1968; Steurbing & Alberdi, 1973; Small, 1972; 1973). Both Arens (1958) and Loveless (1962) suggest that the excessive fibre contents typical of sclerophyllous leaves is due mainly to an absence of adequate phosphate and nitrogen. Thus products of metabolism which otherwise might have formed protein, are diverted along alternative metabolic pathways to form other end products such as fibre.

The trend in the relative importance of leaf texture categories along the NFC is largely consistent with the predictions of Orians and Solbrig's (1977) model. Sclerophylls predominated at the xeric end of the gradient with orthophylls becoming increasingly important at higher altitudes (Fig. 5a). The trend observed for the FC corroborated the nutrient hypothesis as sclerophyll leaves predominated throughout the length of the gradient (Fig. 5a).

In Western Australia Goble-Garrat *et al.* (1981) found no trend in leaf specific weight of heathland plants along a shallow gradient of increasing soil moisture retention.

Spinescence

Fig. 5b shows patterns of leaf and stem spinescence along both coenoclines. Leaf spines predominated in fynbos, possibly because construction costs of leaf spines should be low for species which already have evergreen sclerophyllous leaves (Bond, 1981). Overall, spines were less common in the FC than the NFC probably because of the low nutritional value of fynbos vegetation (Louw, 1969) where low leaf N and P, high fibre content, tannins and phenolics are primary herbivore deterrents (cf. Janzen, 1974; Bond, 1981). In the NFC stem spines predominated throughout the gradient and

declined with increasing altitude; leaf spines at the lower altitudes sites were associated with succulent arborescent Aloe spp. Under drier conditions the cost of rebuilding photosynthetic tissues would be greater than more mesic areas, so that more energy is channeled into deterring herbivores.

Climbers

Climbers allocate little energy to supportive tissue and have forfeited independent support for high growth rates (Givnish & Vermeij, 1976). In this study climbers included woody, herbaceous and succulent species. Patterns of importance in the cover of climbers along both coenoclines are shown in Fig. 5b. They were poorly represented in the FC (a single hemi-parasitic Cassytha ciliolata at site C). Climbers were very common at the lower altitude NFC sites and declined in importance with increasing altitude.

Herbaceous growth forms

Fig. 5c shows the importance of herbaceous growth forms, expressed as a percentage of herbaceous cover, for both coenoclines. Graminoids dominated throughout the FC and other herbaceous growth forms contributed little to herbaceous cover. There was a striking change from dominance by seasonal graminoids (Poaceae) at sites A and B, to non-seasonal graminoids (Restionaceae, Cyperaceae) at sites C - E. This corresponds to the transition from Grassy Fynbos to Mountain Fynbos (Table 3, Fig. 3).

There are two hypotheses to explain this shift in dominance from deciduous to evergreen graminoids. Firstly it can be argued that the deciduous perennial strategy of grasses is dependent on high nutrient reserves for annual replacement of photosynthetic tissue (Specht et al., 1977; Bond, 1981). Therefore grasses would be most common on the slightly more fertile soils of the lower FC sites. A second hypothesis is that the growth of non-seasonal graminoids, particularly Restionaceae, is favoured by cooler growing season temperatures whereas grasses are at a competitive advantage under warmer conditions. At all sites C₄ subtropical grasses predominated and highest cover was recorded on hot north slopes; C₃ temperate grasses were largely confined to cooler south aspects. At sites C and D grasses, mostly C₄ species, were only recorded from north slopes which would receive considerably more radiant energy than other aspects during the wet spring, autumn and winter period. The growing season-temperature

hypothesis also predicts a higher cover of grasses at lower altitudes but does not explain the low cover of C₃ grasses in the cool, moist Mountain Fynbos sites. Experimental studies are required to test the relative effects of nutrients and temperature on the growth of grasses and restioids/cyperoids.

Patterns of herb growth form cover along the NFC were complex and difficult to interpret (Fig. 5c). Non-seasonal graminoids had highest relative cover in the more open and xeric site A. At site B they were replaced by shade tolerant herbs (Acanthaceae) and geophytes (Dietes, Chlorophytum) at sites C - E. Non-seasonal graminoids (Ficinia, Schoenoxiphium) increased in cover towards the high elevation sites.

Phytochorological affinities and endemism

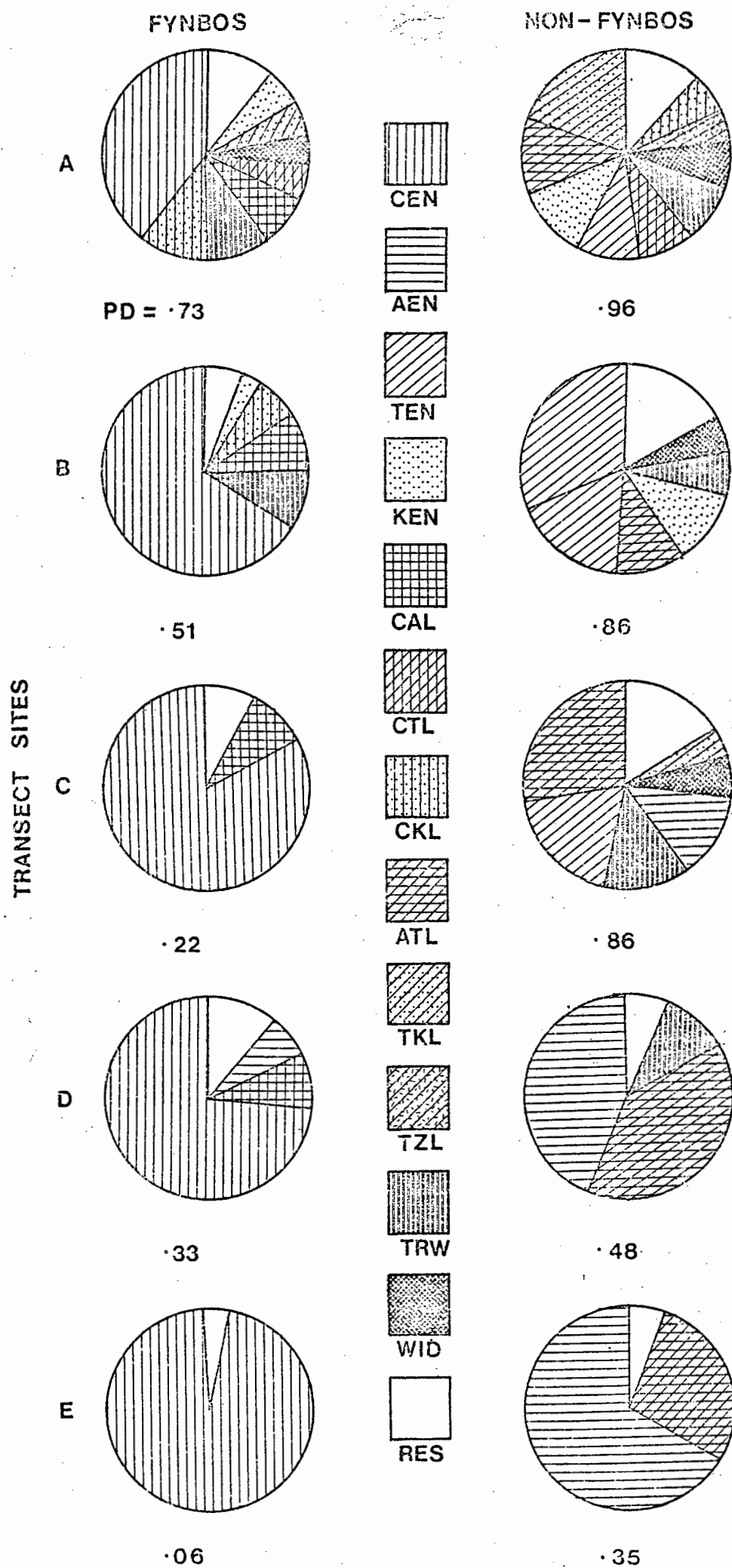
The S.E. Cape comprises a huge tension zone where four major phytochoria converge. Tongaland-Pondoland forest and thicket (Moll & White, 1978) enters the region along the coast and penetrates up the river valleys. Succulent and dwarf shrublands of the Karoo-Namib Region (Werger, 1978b) extend down the dry river valleys from the arid interior. Because of increased latitude compensating for altitude, Afromontane elements are found close to, or at, sea-level. Fynbos taxa of the Cape Region (Taylor, 1978) are strongly represented on the infertile sandy soils derived from Cape Supergroup rocks. The result of this chorological complexity is a mosaic of communities each with different chorological affinities or communities with a chorologically mixed flora. An analysis of the phytochorological affinities and levels of endemism of communities, together with an understanding of climatic change, provides an insight into vegetation history.

Fig. 6 shows phytochorological spectra and values of phytochorological diversity (PD) for sites along both coenoclines. In both the FC and the NFC there was a declining trend in PD with increasing altitude. Fynbos sites were dominated by Cape endemics (CEN) throughout the gradient but chorological transgressor species were common at the lower altitude sites. Particularly important at these lower sites were Cape-Afromontane linking elements (CAL) which indicate the links between Grassy Fynbos and the Afro-montane grasslands of the eastern Cape and Natal (cf. Acocks, 1953). The Grassy Fynbos sites had many tropical-subtropical wides (TRW) which are all subtropical C₄ grasses. Karroid elements were best represented at the low altitude site. The Mountain Fynbos sites (C - E) were overwhelmingly dominated by CEN taxa. I have

Fig. 6.

Phytochorological spectra and values of phytochorological diversity for sample floras of sites in the fynbos and non-fynbos coenoclines.

CEN = Cape endemics, AEN = Afromontane endemics, TEN = Tongaland-Pondoland endemics, KEN = Karoo-Namib endemics, CAL = Cape-Afromontane linking elements, CTL = Cape - Tongaland-Pondoland linking elements, CKL = Cape - Karoo-Namib linking elements, ATL = Afromontane - Tongaland-Pondoland linking elements, TKL = Tongaland-Pondoland - Karoo-Namib linking elements, TZL = Tongaland-Pondoland - Zambezian linking elements, TRW = Tropical-subtropical wides, WID = Wides, RES = residual (phytochorological groups contributing less than 5% of the sample flora).



argued^{that} the less fertile Mountain Fynbos soils comprise an edaphic barrier for the establishment of non-Cape elements, thus explaining the low PD values for the Mountain Fynbos sites (Cowling, 1982a). In the S.E. Cape, Mountain Fynbos is pinched into small patches on the upper seaward facing slopes of the Cape Folded Belt. Because of edaphic barriers to plant migration these areas constitute island-like situations within continental land masses (Wild, 1968; Cowling, 1982).

Along the NFC there is a trend for Tongaland-Pondoland endemics and linking species to decline, and Afromontane elements to increase, with increasing altitude. Highest values for PD were recorded at the low altitude site which had a strong karroid component. Lowest values of PD were recorded in the mesic Afromontane forests which, like Mountain Fynbos, have a patchy island-like distribution in the study area.

Fig. 7 shows patterns of endemism for both coenoclines. Along the FC endemism increased towards the higher altitude sites. Endems were predominantly of Cape affinity although a number of karroid species were recorded in the Grassy Fynbos sites (A and B). The high levels of endemism of Cape taxa suggest that Cape fynbos has had a long history in the S.E. Cape and is not, as suggested by Acocks (1953), derived in historical times from Afromontane grassland or forest. The positive relationship between altitude and endemism of Cape elements ($r = .96$; $p < .01$) indicates the possible role of upper mountain slopes as refugia for fynbos taxa during Pleistocene climatic fluctuations. The existence of endemics of karroid affinity at the lower sites is consistent with the recent developments in climatic modelling for the Cape coastal region which postdict considerably drier glacial conditions than the present Holocene interglacial (Deacon, 1982). During the last glacial karroid vegetation would have been widespread at lower altitudes in the study area, and fynbos would have been confined to the upper elevations where orographic effects would have compensated for the general reduction in rainfall. Changes in rainfall and evapotranspiration would have an important effect on pedogenesis and leaching regimes which, in turn, would have affected the distribution of major vegetation types. The extent and nature of changes in soil properties during a glacial-interglacial sequence is not known.

Along the NFC endemism decreased with increasing altitude. Endems were predominantly karroid taxa which, again, suggests that karoo vegetation was more widespread during the drier glacial. The low numbers of subtropical and Afromontane taxa suggest that these floras have not had a long history in the region. There is some evidence to

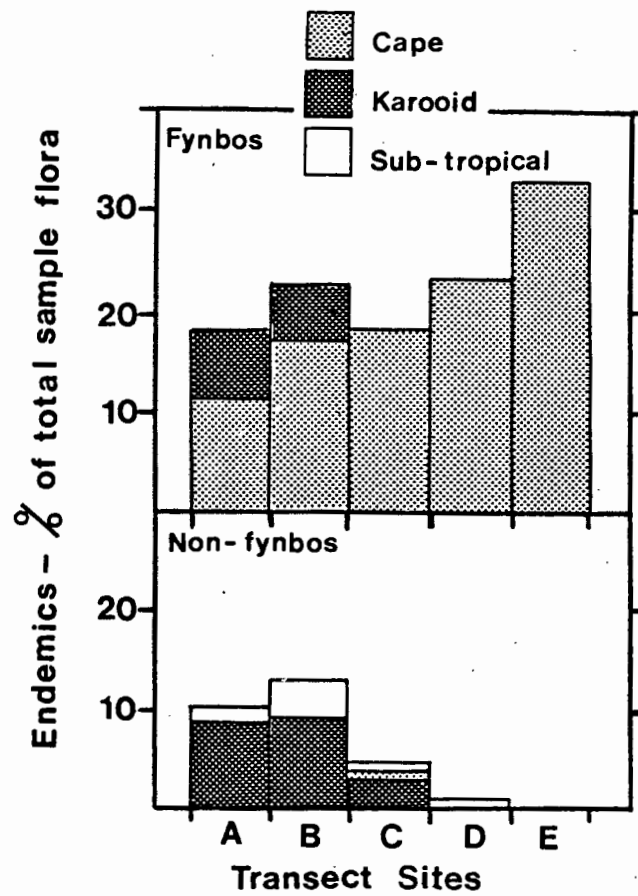


Fig. 7. Taxa endemic to the S.E. Cape expressed as a percentage of the sample flora at sites in the fynbos and non-fynbos coenoclines.

suggest that forest and thicket communities were established in the S.E. Cape only since climatic amelioration after 12,000 B.P. (Deacon, 1982; Cowling, 1982a).

General discussion and conclusions

The hypothesis tested in this study predicts that there would be less structural variation along the FC than the NFC since in the former, the overriding effects of low levels of soil nutrients would result in a great deal of structural convergence in fynbos vegetation. I found much evidence to support this prediction. Along the entire FC the vegetation was a sclerophyllous small-leaved shrubland with a graminoid understorey and, usually, a large-leaved (proteoid) overstorey. The most pronounced change in structure was a shift in dominance from seasonal to non-seasonal graminoids between sites B and C. NFC vegetation ranged from succulent spinescent and sclerophyllous thicket, through non-succulent thicket to tall mesic forest. Patterns in the relative importance of structural attributes and growth forms along the NFC could be interpreted largely in terms of soil moisture and climate; along the FC low levels of nutrients were the paramount factor in determining vegetation structure.

An alternative hypothesis is that the xeromorphic structure of FC vegetation is due to the poor moisture holding capacity of the sandy, shallow, stony and excessively drained fynbos soils. However Bond's (1981) savanna model of fynbos structure predicts that on deeper or more poorly drained soils there would be different patterns in the relative abundance of graminoids and shrubs but the overall structure would remain typically fynbos. These predictions are easily verified (Bond, 1981). I reject the alternative hypothesis but acknowledge that within fynbos, soil moisture can be an important determinant of structure.

It is possible to view certain features of the "heathland syndrome" (Specht, 1979) as non-adaptive. It has been argued that oligotrophic xeromorphic features such as the high fibre content of sclerophyllous leaves are the results of a nutrient limited metabolism (Arens, 1958; Loveless, 1962). In areas where soil moisture is not limiting, sclerophylly on infertile soils could be seen as a non-adaptive feature determined by biochemical constraints (cf. Gould & Lewontin, 1979) imposed on the leaf by ϵ metabolism associated with limiting amounts of certain nutrients.

On the other hand adaptive advantages can be readily inferred, especially for both arid and infertile environments. Small's (1973) hypothesis that there should be a degree of overlap in the ecological amplitude of plants adapted to arid and infertile environments is rejected for the Gamtoos region since there are no species common to the xeric NFC sites and the FC. High molecular weight hydrocarbons such as oils, tannins and phenols, which show high concentrations in the leaves of many fynbos plants (e.g. Smith & Rivett, 1947; Rivett & Woolard, 1967) could also be the products of a nutrient-limited metabolism. However the adaptive significance of these chemicals in deterring herbivory is fairly clear (Janzen, 1974).

Finally I endorse the concern expressed by Gould and Lewontin (1979) at the current practice of atomizing integrated organisms (plants) into parts (leaves, spines) which are then studied as optimized structures, designed by natural selection for their functions (see Parkhurst & Loucks, 1972). I have demonstrated that it is not possible to appreciate fully the significance of different patterns in the importance of leaf texture categories without considering leaf longevity or rooting depth. I believe that future studies should concentrate on whole organisms, their below- and above-ground architecture, their means of regeneration as well as the incidence of the more commonly studied structural attributes. An understanding of form and function in plants will emerge from a study of the whole, rather than from the properties of the parts.

References

- Acocks, J.P.H., 1953. Veld types of South Africa. *Mem. Bot. Surv. S. Afr.* 28.
- Arens, K.O., 1958. Cerrado como vegetação oligotrófica. *Bol. Fac. Fil. Ciênc. Letr. Univ. S. Paulo* 224, *Botânica* 15, 58 - 77.
- Beadle, N.C.W., 1966. Soil phosphate and its role in molding segments of the Australian flora and vegetation with special reference to xeromorphy and sclerophylly. *Ecology* 47 : 992 - 1007.
- Beadle, N.C.W., 1968. Some aspects of the ecology and physiology of Australian xeromorphic plants. *Austr. J. Sci.* 30 : 348 - 355.
- Beals, E.W., 1969. Vegetational change along altitudinal gradients. *Science* 165: 981 - 985.
- Bond, W., 1981. Vegetation gradients in the southern Cape mountains. Unpublished thesis, University of Cape Town, 228 pp.
- Brady, N.C., 1974. The nature and properties of soils. 8th edn. Macmillan, New York. 639 pp.
- Camerik, A.M. & Werger, M.J.A., 1980. Leaf characteristics of the flora of the high plateau of Itatiaia, Brasil. *Biotropica* 13: 39 - 48.
- Campbell, B.M., 1982. Vegetation classification in a floristically complex zone: the Cape Floristic Region. Unpublished ms.
- Campbell, B.M., Cowling, R.M., Bond, W.J. & Kruger, F.J., 1981. Structural characterization of vegetation in the Fynbos Biome. South African National Scientific Programmes Report No. 53. CSIR, Pretoria.
- Chapman, J.D. & White, F., 1970. The evergreen forests of Malawi. Commonwealth Forestry Institute, Univ. of Oxford.
- Cowling, R.M., 1982a. Phytochorology and vegetation history in the south eastern Cape, South Africa. Submitted to *J. Biogeogr.*
- Cowling, R.M., 1982b. A syntaxonomic and synecological study in the Humansdorp region of the Fynbos Biome. Submitted to *Bothalia*.
- Cowling, R.M. & Campbell, B.M., 1980. Convergence in vegetation structure in the mediterranean communities of California, Chile and South Africa. *Vegetatio* 43: 191 - 197.
- Cowling, R.M. & Campbell, B.M., 1982. Defining leaf texture categories in the Fynbos Biome. *Jl. S. Afr. Bot.* (in press).
- Deacon, H.J., 1982. The comparative evolution of mediterranean-type ecosystems: a southern perspective. In: F.J. Kruger, D.T. Mitchell & J.U.M. Jarvis (eds.) *Mediterranean-type ecosystems. The role of nutrients*. Springer, Berlin (in press).

- Edwards, D., 1967. A plant ecology survey of the Tugela Basin, Natal. Mem. Bot. Surv. S. Afr. 36.
- Ferri, M.G., 1961. Problems of water relations of some Brazilian vegetation types with special consideration of the concepts of xeromorphy and xerophytism. Arid Zone Res. XVI Plant water relations in arid and semi-arid conditions. Proc. Madrid Symposium, UNESCO.
- Garland, G.C., 1979. Assymetry in Drakensberg valleys: an alternative point of view. S. Afr. J. Sci. 75: 138 - 139.
- Gates, D., 1968. Transpiration and leaf temperature. Ann. Rev. Plant Physiol. 19: 211 - 238.
- Gibbs Russel, G.E. & Robinson, E.R., 1981. Phytogeography and speciation in the vegetation of the eastern Cape. Bothalia 13: 467 - 472.
- Givinish, T.J. & Vermeij, G.J., 1976. Sizes and shapes of liane leaves. Amer. Natur. 110: 743 - 778.
- Goble-Garrat E.M., Bell, D.T. & Loneragan, W.A., 1981. Floristic and leaf structure patterns along a shallow elevational gradient. Austr. J. Bot. 29: 329 - 347.
- Goldblatt, P., 1978. An analysis of the flora of southern Africa: its characteristics, relationships and origins. Ann. Missouri Bot. Gard. 65: 369 - 436.
- Gould, S.J. & Lewontin, R.C., 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptionist programme. Proc. R. Soc. London B 205: 581 - 598.
- Granger, J.E. & Schulze, R.E., 1977. Incoming solar radiation patterns and vegetation response: examples from the Natal Drakensberg. Vegetatio 35: 47 - 54.
- Grubb, P.J., Lloyd, J.R., Pennington, T.D. & Whitmore, T.C., 1963. A comparison of montane and lowland rain forest in Ecuador. 1. The forest structure, physiognomy and floristics. J. Ecol. 51: 567 - 601.
- Hamilton, A.C., 1975. Quantitative analysis of altitudinal zonation in Uganda forests. Vegetatio 30: 99 - 106.
- Hamman, O., 1979. Climatic conditions, vegetation types and leaf size in the Galapagos Islands. Biotropica 11: 101 - 121.
- Hanawalt, R.B. & Whittaker, R.H., 1976. Altitudinally coordinated patterns of soils and vegetation in the San Jacinto mountains, California. Soil Science 121: 114 - 124.
- Harrison, A.T., Small, E. & Mooney, H.A., 1971. Drought relationships and distribution of two mediterranean climate California plant communities. Ecology 52: 867 - 875.
- Haughton, S.H., Frommurze, H.F. & Visser, D.J.L., 1937. The geology of portions of the coastal belt near the Gamtoos Valley, Cape Province. Geological Survey Report No. 151. Government Printer, Pretoria.

- Hill, M.O., 1973. Reciprocal averaging: an eigenvector method of ordination. *J. Ecol.* 61: 237 - 249.
- Holland, P.G. & Steyn, D.G., 1975. Vegetational responses to latitudinal variations in slope angle and aspect. *J. Biogeogr.* 2: 179 - 183.
- Janzen, D.H., 1974. Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. *Biotropica* 6: 69 - 103.
- Johnson, L.A.S. & Briggs, B.G., 1975. On the Proteaceae - the evolution and classification of a southern family. *Bot. J. Linn. Soc.* 70: 83 - 182.
- Kluge, M. & Ting, I.P., 1978. Crassulacean acid metabolism. Analysis of an ecological adaptation. Springer, Berlin. 209 pp.
- Louw, G.N., 1969. The nutritive value of natural grazings in South Africa. *Proc. S. Afr. Soc. Anim. Prod.* (1969): 57 - 61.
- Louw, W.J., 1976. Mesoclimate of the Port Elizabeth-Uitenhage metropolitan area. Pretoria Weather Bureau Technical Paper No. 4. Government Printer, Pretoria.
- Loveless, A.R., 1962. Further evidence to support a nutritional interpretation of sclerophylly. *Ann. Bot. N.S.* 26: 551 - 561.
- MacVicar, C.N., Loxton, R.F., Lamprechts, J.J.N., Le Roux, J., de Villiers, J.J., Verster, E., Merryweather, F.R., Van Rooyen, T.H. & Von Harmse, H.J., 1977. Soil classification. A binomial system for South Africa. Department of Agricultural Technical Services, Pretoria. 150 pp.
- Miller, P.C., 1982. Canopy structure of mediterranean type shrubs in relation to heat and moisture. In: F.J. Kruger, D.T. Mitchell & J.U.M. Jarvis (eds.) *Mediterranean-type ecosystems. The role of nutrients.* Springer, Berlin (in press).
- Moll, E.J. & White, F., 1978. The Indian Ocean Belt. In: M.J.A. Werger (ed.) *Biogeography and ecology of southern Africa.* Junk, The Hague.
- Moll, E.J., McKenzie, B. & MacLachlan, D., 1980. A possible explanation for the lack of trees in the fynbos, Cape Province, South Africa. *Biol. Conserv.* 17, 221 - 228.
- Monk, C.C., 1966. An ecological significance of evergreenness. *Ecology* 47: 504 - 505.
- Mooney, H.A., 1982. Carbon-gaining capacity and allocation patterns of mediterranean-climate plants. In: F.J. Kruger, D.T. Mitchell & J.U.M. Jarvis (eds.) *Mediterranean-type ecosystems. The role of nutrients.* Springer, Berlin (in press).
- Mooney, H.A. & Dunn, E.L., 1970. Convergent evolution of mediterranean-climate evergreen sclerophyll shrubs. *Evolution* 24: 292 - 303.

- Mooney, H.A., Gulmon, S.L. & Parsons, D.J., 1974. Morphological changes within the chaparral vegetation types as related to elevational gradients. *Madrono* 22: 281 - 285.
- Mooney, H.A., Harrison, A.T., Morrow, P.A., 1975. Environmental limitations of photosynthesis on a California evergreen shrub. *Oecologia* 19: 293 - 301.
- Mooney, H.A., Troughton, J.H. & Berry, J.A., 1977. Carbon isotope ratio measurements of succulent plants in southern Africa. *Oecologia* 30: 295 - 305.
- Mooney, H.A., Ferrar, P.J. & Slatyer, R.O., 1978. Photosynthetic capacity and carbon allocation patterns in diverse growth forms of Eucalyptus. *Oecologia* 36, 103 - 111.
- Moore, P., 1980. The advantages of being evergreen. *Nature* 285 : 535.
- Morrow, P.A. & Mooney, H.A., 1974. Drought adaptations in two California evergreen sclerophylls. *Oecologia* 15: 205 - 222.
- Orians, G.H. & Solbrig, O.T., 1977. A cost-income model of leaves and roots with special reference to arid and semi-arid areas. *Amer. Natur.* 111: 677 - 690.
- Parkhurst, D.F. & Loucks, O.L., 1972. Optimal leaf size in relation to environment. *J. Ecol.* 60: 505 - 537.
- Parsons, D.J., 1976. Vegetation structure in the mediterranean scrub communities of California and Chile. *J. Ecol.* 64: 435 - 447.
- Parsons, D.J. & Moldenke, A.R., 1975. Convergence in vegetation structure along analogous climatic gradients in the mediterranean climate ecosystems of California and Chile. *Ecology* 56: 950 - 957.
- Peet, R.K. & Loucks, O.L., 1977. A gradient analysis of southern Wisconsin forests. *Ecology* 58: 485 - 499.
- Pierce, S.M. & Cowling, R.M., 1982. Phenology of fynbos and non-fynbos communities in the south eastern Cape. Unpublished MS.
- Raunkiaer, C., 1934. The life forms of plants and statistical plant geography. Oxford Univ. Press, Oxford.
- Richards, P.W., 1964. The tropical rain forest. University Press, Cambridge.
- Rivett, D.E.A. & Woolard, G.R., 1967. The structure of Euryopsonol. *Tetrahedron* 23: 2431 - 2436.
- Rutherford, M.C., 1978. Karoo-fynbos biomass along an elevational gradient in the western Cape. *Bothalia* 12: 555 - 560.
- Schimper, A.F.W., 1903. Plant geography on a physiological basis. Clarendon Press, Oxford.
- Schulze, R.E., 1975. Incoming radiation fluxes on sloping terrain: a general model for use in southern Africa. *Agrochimophysica* 7: 55 - 60.

- Small, E., 1972. Ecological significance of four critical elements in plants of raised sphagnum peat bogs. *Ecology* 53: 489 - 503.
- Small, E., 1973. Xeromorphy in plants as a possible basis for migration between arid and nutritionally deficient environments. *Bot. Notiser* 126: 534 - 539.
- Smith, J.L.B. & Rivett, D.E.A., 1947. The essential oil of Agathosma gnidiodes Schlechter. *Trans. Roy. Soc. S. Afr.* 31: 333 - 345.
- Specht, R.L., 1979. Heathlands and related shrublands of the world. In: R.L. Specht (ed.) *Heathlands and related shrublands of the world, vol. A. Descriptive studies*, p. 1 - 19. Elsevier, Amsterdam.
- Specht, R.L., Connor, D.J. & Clifford, H.T., 1977. The heath-savannah problem. The effect of fertilizers on sand-heath vegetation of North Stradbroke Island, Queensland. *Austr. J. Ecol.* 2: 179 - 186.
- Steubing, L. & Alberdi, M., 1973. The influence of phosphorus efficiency on sclerophylly. *Oecologia plantarum* 8: 211 - 218.
- Taylor, S.E., 1975. Optimal leaf form. In: D.M. Gates & R.B. Schmerl (eds.) *Perspectives of biophysical ecology*, p. 73 - 86. Springer, Berlin.
- Taylor, H.C., 1978. Capensis. In: M.J.A. Werger (ed.) *Biogeography and ecology of southern Africa*, p. 171 - 229. Junk, The Hague.
- Walter, H., 1979. *Vegetation of the earth and ecological systems of the geobiosphere*. 2nd ed. Springer, Berlin.
- Webb, L.J., 1959. A physiognomic classification of Australian rain forests. *J. Ecol.* 47: 551 - 570.
- Weimarck, H., 1941. Phytogeographical groups, centres and intervals within the Cape Flora. *Lund Universiteits Arsskrif. N.F. Adv. Z. Bd.* 37, Nr 5: 1 - 143.
- Werger, M.J.A., 1978a. Biogeographical division of southern Africa. In: M.J.A. Werger (ed.) *Biogeography and ecology of southern Africa*, p. 147 - 170. Junk, The Hague.
- Werger, M.J.A., 1978b. The Karoo-Namib Region. In: M.J.A. Werger (ed.) *Biogeography and ecology of southern Africa*, p. 233 - 299. Junk, The Hague.
- Werger, M.J.A. & Ellenbroek, G.A., 1978. Leaf size and leaf consistence of a riverine forest formation along a climatic gradient. *Oecologia* 34: 297 - 308.
- White, F., 1978. The Afromontane Region. In: M.J.A. Werger (ed.) *Biogeography and ecology of southern Africa*, p. 465 - 510. Junk, The Hague.
- Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* 30: 279 - 338.
- Whittaker, R.H., 1967. Gradient analysis of vegetation. *Biol. Rev.* 42: 207 - 264.

- Whittaker, R.H., 1973. Direct gradient analysis: techniques and results.
In: R.H. Whittaker (ed.) Ordination and classification of communities,
p. 7 - 51. Junk, The Hague.
- Whittaker, R.H. & Niering, W.A., 1968. Vegetation of the Santa Catalina
Mountains, Arizona. IV. Limestone and acid soils. *J. Ecol.* 56: 523 - 544.
- Whittaker, R.H., Gilbert, L.E. & Connel, J.H., 1979. Analysis of two phase
pattern in a mesquite grassland, Texas. *J. Ecol.* 67: 935 - 952.
- Wild, H., 1968. Phytogeography of south central Africa. *Kirkia* 6: 197 - 222.

GENERAL CONCLUSIONS

Many of the aims of this study were achieved. Detailed discussions of the conclusions are not included in this section: summaries of these are to be found at the end of each paper and in the abstracts. I wish rather to express my views on directions for future research in the Fynbos Biome. My study fits squarely in a descriptive framework with a bent towards dynamics, history and an adaptationist view of plant forms and function. I discuss below what I believe should be the major focus of a post-descriptive phase in fynbos research.

It seems that ecological theory is now at a crucial crossroad. We have witnessed the demise of bold deductive theories in the face of indisputable falsifying evidence. We are advised, on one hand, to shed our obsession with deterministic models in ecology and to acknowledge openly the unexplained residua and variability of ecological data, not as "noise" but as "music" (Simberloff 1980). On the other hand Harper (1980; 1982) argues forcibly in favour of a reductionist approach, which concentrates on the lives and deaths of individual plants, as the key to understanding the distribution and abundance of plants and the evolutionary forces which have determined (or constrained) their form and function. We are advised to become agriculturalists, to study monocultures and simple, species-poor pastures; or gardeners, transplanting species to different environments to understand what restricts them to the place where they grow naturally (Harper 1980). I do not doubt that many ecological generalizations will emerge from the study of the demography of individual plants. However the Fynbos Biome is a very large garden.

Conservation and management are the principal aims of the Fynbos Biome Project. Therefore we must acquire a predictive knowledge of the dynamics of fynbos and related shrublands in response to the most common perturbation, fire. As I see it there are two approach options. We can conduct lengthy experiments by applying different fire regimes to different communities, and through the proper use of controls we can then determine the effects of these fire regimes on community structure. The sacrifice of these inductively derived dynamic models is generality (Goodall 1977). The predictions of these models cannot be extrapolated confidently to areas other than where the experiments were conducted. A second approach would be to study the regeneration niches (Grubb 1977) of individual species. This is basically a vital attributes (Noble and Slatyer 1980) reductionist approach which will enable us to predict the effects of various fire regimes on community structure provided we have data on most species and can safely

assume little genotypic variability in reproductive parameters across the distribution range of the species. Experiments can then be designed to validate these predictions.

It is estimated that there are 8 550 species in the Cape Floristic Region (Goldblatt 1978) and most of these are confined to fire-prone shrublands. Clearly we are faced with the formidable task of collecting the appropriate data if we are to adopt the second approach outlined above. I predict tremendous diversity of regeneration niches in fynbos shrublands and suspect that this could partly explain fynbos diversity. We must restrain ourselves from concentrating our efforts on the more glamorous or conspicuous components of the vegetation: the current practice of prescribing burning programmes in the fynbos which are geared towards the maintenance of Proteaceae populations should be re-evaluated.

Perhaps an ultimate though optimistic objective should be a classification of species into physiological-structural-reproductive types. This implies groupings of species with similar regeneration niches, below- and above-ground architecture, canopy characteristics, carbon gain phases and phenophases. This approach demands the study of whole plants as integrated entities where physiology, structure and reproduction are linked together. It will not raise the problems associated with the adaptionist view of atomizing organisms into optimized parts whose "adaptive significance" is then interpreted in terms of the omnipotent forces of natural selection (Gould and Lewontin 1979). This "whole-plant" approach will reveal the evolutionary constraints on plant form and function and hopefully guide us beyond "facile adaptionist guesswork" (Harper 1982).

This is not to say that there is no need for further descriptive studies in the biome. There is little phytosociological data on most biome vegetation types, particularly inland Transitional Small-leaved Shrublands and Mountain Fynbos. Although structural classifications will go a long way in providing meaningful vegetation units for management purposes (Campbell in prep.), I believe that a floristic syntaxonomy should be a long term objective.

The history of biome vegetation types is largely a mystery. Studies on vegetation history are necessarily multi-disciplinary, involving aspects of palaeoclimatic modelling, palaeoecological investigations, evolutionary systematics and plant geography.

The growth of knowledge on this subject will depend on how quickly we move away from anecdotal narrative explanations to generalized explanations which yield sound testable predictions. (Ball 1976). The latter will stimulate research by encouraging workers from different disciplines to test these hypotheses using independent lines of evidence.

References

- Ball I R 1976. Nature and formulation of biogeographic hypotheses. Systematic Zoology 24, 407 - 430.
- Campbell B M in prep. Vegetation classification in a floristically complex zone : The Cape Floristic Region.
- Goldblatt P 1978. An analysis of the flora of southern Africa: its characteristics, relationships and origins. Annals of the Missouri Botanical Garden 65, 369 - 436.
- Goodall D W 1977. Dynamic changes in ecosystems and their study: the roles of induction and deduction. Journal of Environmental Management 5, 309 - 317.
- Gould S J and R C Lewontin 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptionist programme. Proceedings of the Royal Society of London. B. 205, 581 - 598.
- Grubb P J 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. Biological Review 52, 107 - 145.
- Harper J L 1980. Plant demography and ecological theory. Oikos 35, 235 - 244.
- Harper J L 1982. After description. The plant community as a working mechanism. Special publication of the British Ecological Society number 1. Blackwell, London. pp 11 - 25.
- Noble I R and R O Slatyer 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43, 5 - 21.
- Simberloff D 1980. A succession of paradigms in ecology: essentialism to materialism to probabilism. Synthese 43, 3 - 39.

APPENDIX 1

THE OCCURRENCE OF C₃ AND C₄ GRASSES IN FYNBOS AND ALLIED SHRUBLANDS IN THE SOUTH EASTERN CAPE, SOUTH AFRICA

SUMMARY

There are roughly equal numbers of C₃ and C₄ grass species in fynbos and allied shrublands of the warm temperate coastal regions of the south eastern Cape. Subtropical - tropical C₄ species have the highest relative cover in all shrubland types, particularly in renosterveld communities on moderately fertile soils. Physiological characteristics of C₃ and C₄ grasses predict that C₃ species will be most abundant in cool, shaded sites. This prediction, and the hypothesis that relative C₃ grass cover would be highest on infertile soils, were tested by correlation and regression analyses. Results show that C₃ grass cover is significantly correlated with increased post-disturbance vegetation age, low intensity grazing, high litter cover and cool, steep, poleward slopes. All these factors contribute to lower growing season temperatures, favouring the competitive growth of C₃ species. Amongst the soil variables, high sand content and low levels of total nitrogen emerged as predictors of high relative C₃ grass cover.

INTRODUCTION

Plants having the C_4 photosynthetic pathway differ from C_3 plants in their anatomy, physiology and ecological requirements (Black 1971, 1973, Laetsch 1974). C_4 photosynthesis can have significant advantages over the C_3 mode under conditions of high light intensities, high temperatures and low intercellular CO_2 concentrations (Black 1971, Björkman 1975). Recently Ehleringer and Björkman (1977) have shown that the quantum yield is greater for C_3 plants at low temperatures and that the C_4 pathway should be disadvantageous under these conditions. Simulation studies by Ehleringer (1978) incorporating the effects of temperature on quantum yields of C_3 and C_4 grasses were able to predict accurately the higher relative abundance of C_4 species in high light and temperature environments. Some exceptions to these eco-physiological generalizations have been reported (e.g. Caldwell et al. 1977) but differences appear to be consistent within the Poaceae (Ode et al. 1980).

A number of studies have investigated the factors responsible for the distribution of C_3 and C_4 grasses along selected environmental gradients (Chazdon 1978; Tiezen et al. 1979; Boutton et al. 1980, Rundel 1980) and within broad geographical regions (Teeri and Stowe 1976, Vogel et al. 1978, Ellis et al. 1980). Certain of these studies report that both temperature and rainfall are equally reliable as predictors of the relative occurrence of C_3 and C_4 grasses (Chazdon 1978, Tiezen et al. 1979, Boutton et al. 1980). Others, including a study on the distribution of C_4 grasses in South Africa (Vogel et al. 1978), indicate that the temperature during the growing season is the major climatic factor accounting for the distribution and abundance of C_3 and C_4 species (see also Teeri and Stowe 1976, Ellis et al. 1980).

In this paper I report on the occurrence of C_3 and C_4 grass species in fynbos and allied shrubland in the Humansdorp region of the south eastern Cape, and test hypotheses to explain patterns in their relative abundance. I focussed on the role of microclimate as there is little variation in annual precipitation and elevation in the study area. I also investigated the role of soil nutrients, following the observation by Bond (1981) that in the southern Cape mountains C_4 grass cover is highest on sites with fertile soils. The hypotheses tested were: 1) that the relative cover of C_3 grasses would be highest in cool shaded sites, and 2) that the relative C_3 grass cover would be higher on infertile soils.

STUDY AREA

The study area is in the Humansdorp district of the south eastern Cape on the eastern boundary of the Fynbos Biome (Kruger 1978) (Fig. 1). It forms part of the Cape coastal forelands, a marine and continental planed surface which cuts across a number of geological formations. Topography is generally subdued (0 - 200m) although some east trending remnant anticlines of the Cape Folded Belt reach an altitude of 400m.

The geology is dominated by rocks of the Cape Supergroup. Much of the area is comprised of quartzitic sandstones of the Table Mountain Group (T.M.G.). Soils are sandy, acid and infertile. Shales of the Bokkeveld Group have moderately fertile sandy loam to loam soils. Cretaceous conglomerates of the Uitenhage Group occur to the north and east of the study area. Soils are moderately fertile, stony, loamy sands. Along the coast there are deposits of Recent sediments and soils are neutral to alkaline, calcareous sands. Soil data are shown in Table 1.

The Humansdorp district has a climate transitional between Köppen Cfb and Csb climates (c.f., Schulze and McGee 1978). The temperature regime is warm temperate and rain can fall at any time of the year although the three summer months (Dec. to Feb.) are always the driest (Fig. 2). There is little variation in annual precipitation and temperature in the study area and the climate diagram for Cape St. Francis (Fig. 2) summarizes climatic conditions adequately. A higher rainfall (700 - 750 mm yr⁻¹) and possibly cooler temperatures would be recorded on the low quartzite hills (300 - 400m) north west of Humansdorp (Fig. 1). The warmest month at Cape St. Francis is February (mean monthly temperature of 19.9°C) and the coolest is July (14.2°C). The months with the highest and lowest mean absolute maxima are April (29.7°C) and August (5.0°C). (Anon. 1942).

The vegetation has been described in detail by Cowling (1982). The shrublands I sampled for this study are typical of the Cape region (Taylor 1978). They comprise two shrubland classes: Cape Fynbos Shrublands and Cape Transitional Small-leaved Shrublands. The former occur on quartzites (Grassy Fynbos) and dune sands (South Coast Dune Fynbos) (Table 1). Structurally they are small leaved or proteoid shrublands (Campbell et al. 1981) and have many features characteristic of heathlands (Specht and Moll 1982). Typical Grassy Fynbos shrub species are Protea neriifolia, Leucadendron salignum, Leucospermum cuneiforme, Erica pectinifolia and Anthospermum aethiopicum. Dominant Dune Fynbos shrubs are Agathosma stenopetala, Passerina vulgaris, Erica

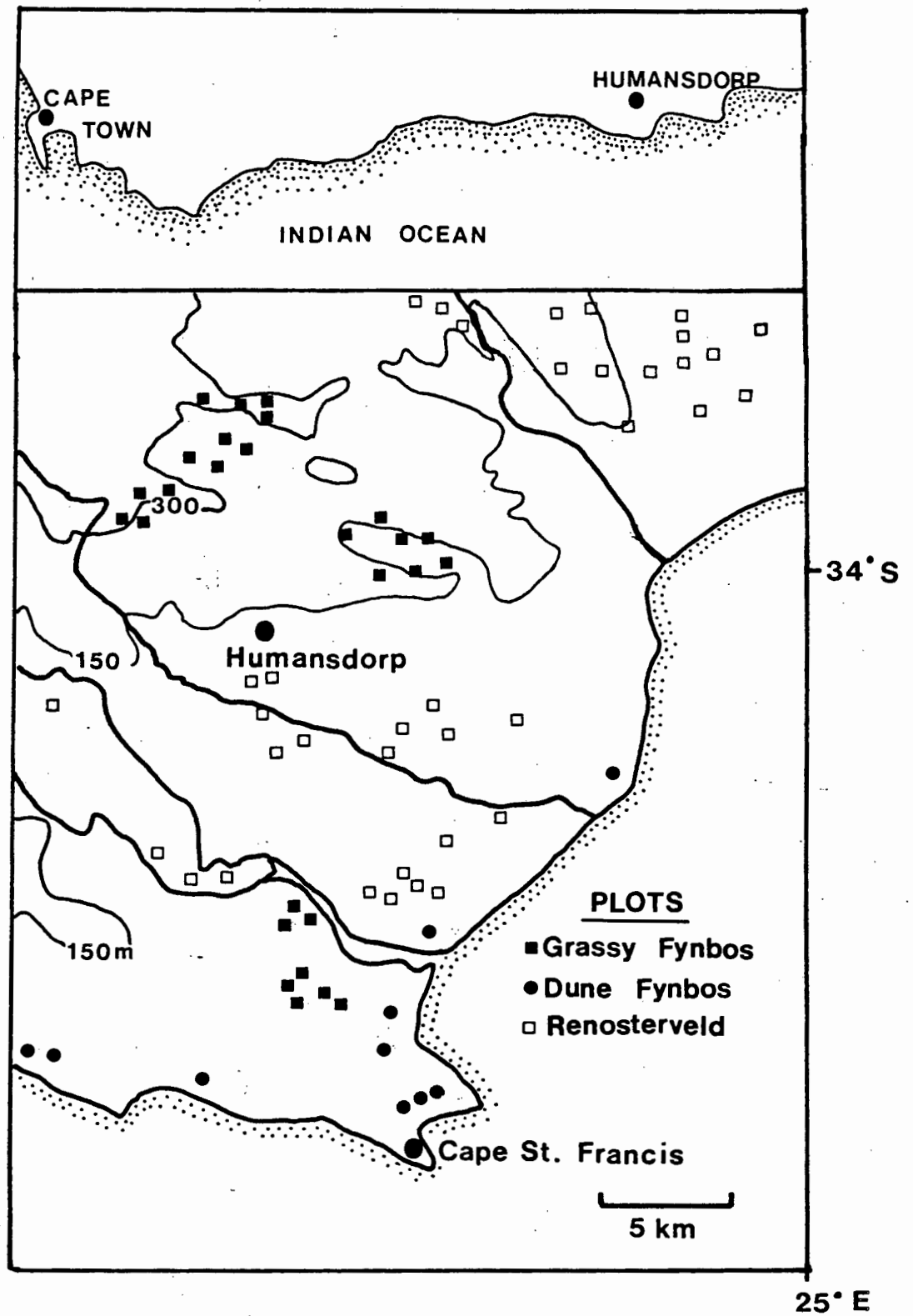


Fig. 1 The location of the study area

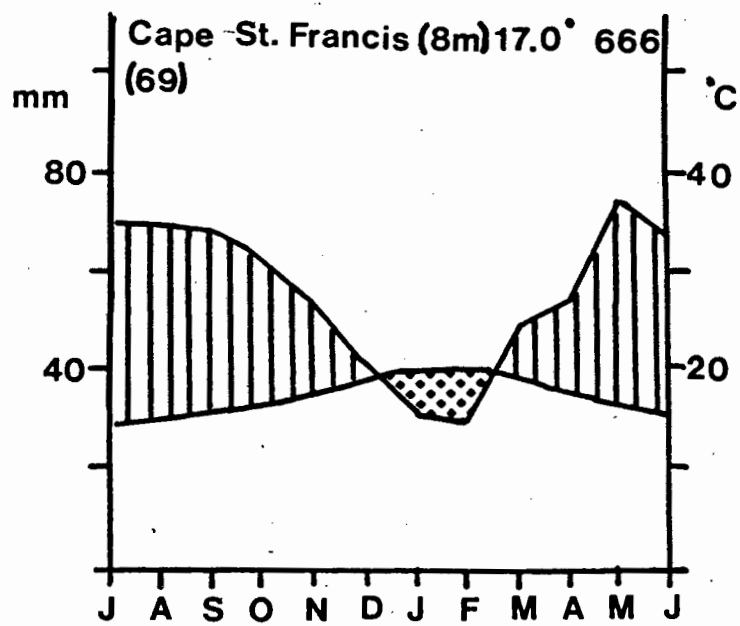


Fig. 2 Walter-Lieth climate diagram for Cape St. Francis. At Humansdorp (152m) only precipitation is recorded (667 mm yr^{-1} , $n = 29$). Data from Anon (1942) and Weather Bureau (1954)

Table 1. Soil data for shrubland types in the study area. Values shown are means ⁺ standard deviations.
See Table 2 for methods of soil analysis

	n	Parent material	% sand	pH	S-value ^a (meq %)	Exchangeable calcium (ppm)	Oxidizable carbon (%)	Total Nitrogen (%)	Available phosphorus (ppm)
<u>Cape Fynbos Shrublands</u>									
Grassy Fynbos	14	Quartzite	89.7 [±] 9.7	4.6 [±] 0.3	3.7 [±] 1.6	403 [±] 203	4.3 [±] 2.1	0.11 [±] 0.05	3.5 [±] 2.2
South Coast Dune Fynbos	6	Dune sands	97.8 [±] 3.7	7.3 [±] 0.7	13.4 [±] 4.6	2311 [±] 775	5.3 [±] 3.6	0.19 [±] 0.12	22.5 [±] 13.7
<u>Cape Transitional Small-leaved Shrublands</u>									
South Coast Renosterveld	12	(i) Shale	60.4 [±] 7.0	5.1 [±] 0.4	7.9 [±] 2.5	758 [±] 287	5.7 [±] 2.6	0.20 [±] 0.06	4.4 [±] 2.9
	6	(ii) Conglomerate	88.1 [±] 11.5	4.8 [±] 0.2	7.7 [±] 1.2	989 [±] 314	7.3 [±] 0.7	0.22 [±] 0.02	5.9 [±] 1.9
	<u>38</u>								

^a

Sum of exchangeable cations

glumiflora, Muraltia squarrosa and Rhus spp. In both fynbos types the herbaceous understorey is dominated by Restionaceae, Poaceae and Cyperaceae. Cape Transitional Small-leaved Shrublands include South Coast Renosterveld which is putatively derived in historical times from grassland (Cowling 1982). Renosterveld occurs on the moderately fertile shales and conglomerates (Table 1). Dominant shrubs are Elytropappus rhinocerotis, Cliffortia linearifolia, Metalasia muricata, Relhania genistaefolia and Passerina rubra. Grasses predominate in the field layer.

In the study area these shrubland types are burnt or bush-cut on a 4 to 5 yr rotation and grazed by domestic livestock. A few 10–12 yr relic stands are found in locally protected sites. The result is that within each Shrubland type there are a range of structural cover states ranging from grasslands (immature) to closed shrublands (mature).

METHODS

I sampled 74 100m² (10 x 10m) plots to reflect the full range of community types and disturbance regimes in the study area. I estimated percentage canopy cover of each grass species and recorded total grass cover as a percentage of the total vegetal cover. The cover of C₃ and C₄ grasses was expressed as a proportion of the total grass cover. Photosynthetic pathway of grasses is according to Ellis (1977), Vogel et al. (1978) and R. Ellis (personal communication). In each plot I recorded a range of environmental variables. These are shown in Table 2, along with classes of variables and some details on methods.

I used stepwise multiple linear regressions computed by forward selection (Allen and Learn 1973) using all environmental factors as independent variables against the relative cover of C₃ grasses. I performed independent analyses on the full data set excluding soil chemical variables (n = 74) and for the subset including soil chemical data (n = 38). The use of proportional grass cover means that the relationships for C₃ grasses are exactly the inverse of those for C₄ grasses. All values of r are Pearsons correlation coefficient.

Table 2. Environmental variables recorded in plots ($n = 74$). Soil chemical data for the A horizon only, from a subset of 38 samples. Abbreviations are those used in the text and Tables 5 and 6. Some details on methods and classes of variables are given.

VAG	VEGETATION AGE	Post-fire, post bushcut. Estimates in years are based on information from landowners.
GRZ	GRAZING INTENSITY	Classes: ungrazed = 1, light = 2, moderate = 3, heavy = 4, overgrazed = 5. Scale based on current stocking rate, past grazing intensity and the effects of grazing (cf. Roberts et al. 1975).
ALT	ALTITUDE	1 : 50 000 topographic sheets
RAI	ANNUAL RAINFALL	1 : 250 000 isohyet maps and local weather stations.
ASP	ASPECT	Classes: 1 = SE, 2 = S, 3 = SW, 4 = E, 5 = W, 6 = NE, 7 = N, 8 = NW. A cool to hot gradient estimated from aspect - radiation flux data (Schulze 1975).
SLO	SLOPE INCLINATION	
RCO	ROCK COVER (%)	
SDE	SOIL DEPTH (m)	
LIT	LITTER COVER (%)	
SAN	% SAND CONTENT	Pipette method.
PHH	pH IN KCl	1 : 2.5 soln.
CAC	EXCHANGEABLE CALCIUM	} 1 N NH_4 acetate leachate
BAS	S VALUE Sum of exchangeable cations	
CAR	OXIDIZABLE CARBON	Walkley-Black method
NIT	TOTAL NITROGEN	Kjeldahl
PHO	AVAILABLE PHOSPHORUS	Bray No. 2 (acid extraction, pH 3) Modified Olsen (alkali extraction, pH 8)

RESULTS AND DISCUSSION

Table 3 shows the photosynthetic pathway and geographical affinity of grasses in the shrublands of the study area. C_3 and C_4 species were equally common. The former are largely of Cape and Afromontane affinity (see Clayton 1976, Taylor 1978) and belong mainly to temperate tribes. C_4 species are mostly widespread in subtropical and tropical Africa.

Total relative grass cover was highest in the renosterveld communities and lowest in the fynbos (Table 4). In the latter communities grasses are partially replaced by Restionaceae (Restio, Thamnochortus and Hypodiscus) and Cyperaceae (Ficinia and Tetraria). High standard deviations of means of relative grass cover reflect the range of structural cover states in communities subjected to recurrent disturbances where grass cover declines with increasing age of the vegetation stand (Cowling 1982). C_4 species comprised most of the grass cover in all communities although values were lowest in fynbos shrublands; the relative cover of C_3 species was particularly low in shale renosterveld (Table 4). The greatest number of both C_3 and C_4 species was found in Grassy Fynbos (Table 4) which included 72% of the total grass flora. Lowest grass diversity ^{was} in the shale renosterveld and Dune Fynbos.

The results of the correlation analysis are shown in Table 5. Vegetation age (VAG) emerged as a factor showing strong positive correlations with C_3 grass cover (and inversely a negative correlation with C_4 grass cover). In mature vegetation there is increased shading of the field layer by overstorey shrubs resulting in reduced soil surface temperatures. Self shading by moribund grasses would also contribute to lower soil temperatures (see Rice and Parenti 1978) thus favouring the growth of C_3 grasses which have relatively lower optimum temperatures for growth (Black 1971). The fairly strong positive correlation with soil litter (LIT) also illustrated the importance of reduced soil temperatures. LIT showed strong positive relationships with VAG ($r = .56$, $P < .001$, $n = 74$; $r = .52$, $P < .001$, $n = 34$). In mature vegetation an accumulation of litter, particularly moribund grass material, reduces soil temperature which can have a marked effect on the growth of C_4 grasses as shoot apices and tillers lie close to the soil surface (Evans et al. 1964, Rice and Parenti 1978).

Table 3. Taxonomy ^a, photosynthetic pathway and geographical affinity of grasses in fynbos and allied shrublands of the study area

C ₃ species	Tribe	Geographical affinity
<u>Ehrharta capensis</u> <u>E. ramosa</u> <u>E. calycina</u> <u>E. villosa</u>	Ehrharteae	Afrotemperate : Cape
<u>Festuca scabra</u> <u>F. caprina</u>	Festuceae	Afrotemperate : Afromontane
<u>Melica racemosa</u> <u>M. decumbens</u>	Meliceae	Afrotemperate : Afromontane
<u>Helictotrichon hirtulum</u> <u>Koeleria capensis</u>	Aveneae	Afrotemperate : Cape Afrotemperate : Cape-Afromontane
<u>Plagiochloa uniolae</u> <u>Lasiochloa longifolia</u> <u>L. obtusifolia</u> <u>Karoochloa curva</u> <u>Merxmüllera stricta</u> <u>M. disticha</u> <u>Pentaschistis angustifolia</u> <u>P. curvifolia</u> <u>P. eriostoma</u> <u>P. heptamera</u> <u>P. involuta</u> <u>P. fortuosa</u> <u>P. airoides</u>	Danthonieae	Afrotemperate : Cape " " " " " " Afrotemperate : Cape-Afromontane Afrotemperate : Cape-Afromontane Afrotemperate : Cape " " " " " " " " " " " "
C ₄ species		
<u>Eragrostis curvula</u> <u>E. capensis</u>	Eragrosteae	Subtropical - Tropical Africa " " "
<u>Harpochloa falx</u> <u>Eustachys paspaloides</u> <u>Cynodon dactylon</u>	Chlorideae	Afrotemperate : Afromontane Subtropical - Tropical Africa " " "
<u>Sporobolus africanus</u> <u>S. fimbriatus</u> <u>S. centrifugus</u>	Sporoboleae	Subtropical - Tropical Africa " " " Afrotemperate : Afromontane
<u>Tristachya leucothrix</u>	Arundinelleae	Subtropical - Tropical Africa
<u>Stipagrostis zeyheri</u> subsp. <u>zeyheri</u> <u>Aristida junciformis</u>	Stipeae	Cape - Subtropical Africa Subtropical - Tropical Africa
<u>Setaria flabellata</u> <u>Digitaria eriantha</u> <u>Stenotaphrum secundatum</u> <u>Brachiaria serrata</u> <u>Rhyncelytrum setifolium</u>	Paniceae	Subtropical - Tropical Africa " " " " " " " " " " " "
<u>Imperata cylindrica</u> <u>Themeda triandra</u> <u>Diheteropogon filifolius</u> <u>Cymbopogon marginatus</u> <u>Heteropogon contortus</u> <u>Trachypogon spicatus</u> <u>Elionurus mutica</u>	Andropogoneae	Subtropical - Tropical wide Subtropical - Tropical wide Afrotemperate : Afromontane Cape - Subtropical Africa Subtropical - Tropical wide Subtropical - Tropical Africa Subtropical - Tropical wide

^a Taxonomy follows Gibbs Russell and Smook (1980) and Meredith (1955).

Table 4. Mean grass cover (%) and number of species of C₃ and C₄ grasses in 100m² plots in fynbos and allied shrublands. Relative grass cover and species richness are shown as means \pm standard deviations

	n	Total relative grass percentage cover ^a	C ₃			C ₄		
			Relative cover ^b	Total no. species	No. species/ 100m ²	Relative cover ^b	Total no. species	No. species/ 100m ²
Grassy Fynbos	27	35.9 [±] 16.1	37.1	16	3.0 [±] 1.5	62.9	17	5.5 [±] 4.4
South Coast Dune Fynbos	10	40.7 [±] 36.3	29.7	4	1.6 [±] 0.7	70.3	11	4.3 [±] 1.8
South Coast Renosterveld								
(i) Shale	24	53.2 [±] 25.6	13.1	7	1.7 [±] 1.3	86.9	9	3.9 [±] 1.5
(ii) Conglomerate	13	52.9 [±] 16.7	24.1	9	2.1 [±] 0.8	75.9	13	5.9 [±] 1.6
	74							

a Cover expressed as a percentage of the total vegetal cover

b Cover expressed as a percentage of the total grass cover

Grazing intensity (GRZ) showed negative correlations with relative C₃ grass cover. The effect of grazing is to remove grass material and thus exposes shoot apices to greater insolation resulting in higher temperatures. GRZ was strongly correlated with LIT ($r = - .47$, $P < .001$, $n = 74$; $r = - .55$, $P < .001$, $n = 38$) and VAG ($r = - .57$, $P < .001$, $n = 74$; $r = - .57$, $P < .001$, $n = 38$).

Amongst the topographical variables aspect (ASP), altitude (ALT) and slope (SLO) were highly correlated with relative C₃ grass coverage. Sites with poleward aspects were favoured as evinced by strong negative C₃ grass - ASP relationships. During the spring, winter and autumn months solar radiation at latitude 34°S is strongly influenced by a lower noon sun azimuth resulting in a marked decrease in radiation on south aspects (Schulze 1975, Holland et al. 1977). The cooler temperatures on south slopes during these months, when soil moisture conditions are probably optimal for growth (Fig. 1), explains the higher relative cover of C₃ grasses in these sites. Conversely C₄ grass cover is higher on north slopes where higher radiation loads are experienced.

It is possible that lower temperatures associated with higher altitudes explain the higher relative cover of C₃ grasses in these sites. Scharf (1979) has measured an environmental lapse rate of 0.6°C per 100m in the Great Winterhoek Mountains, 50 km north east of Humansdorp. This means a 2.4°C difference in average annual temperature between sea level (Cape St. Francis) and the highest elevation in the study area (c. 400m).

ALT shows strong relationships with ASP ($r = - .40$, $P < .001$, $n = 74$; $r = - .44$, $P < .01$, $n = 38$) and SLO ($r = .49$, $P < .001$, $n = 74$; $r = .49$, $P < .01$, $n = 38$). Although SLO is uncorrelated with ASP, all of the high altitude plots are on steep south slopes of the low hills where I recorded high relative C₃ grass cover. I did not sample steep high altitude north slopes as the community types on these warm sites are identical to the adjacent lowlands. I have subsequently observed that these areas are dominated by C₄ species, indicating the overriding influence of increased radiation loads.

There was a weak positive correlation between percentage sand (SAN) and C₃ grass cover. In the Fynbos Biome high sand content is largely associated with infertile soils derived from T.M.G. quartzites (Lamprechts, 1979). However in the study area this relationship is obscured by the moderately fertile dune sands and sandy soils derived from conglomerates. With the exception of total nitrogen (NIT) ($r = - .44$, $P < .02$, $n = 38$) there were no negative correlations between SAN and variables reflecting soil fertility. NIT was the only soil chemical variable negatively correlated with C₃ grass

Table 5. Environmental variables with which relative C_3 grass coverage is correlated with $P < .05$. Values in table are Pearsons r . See Table 2 for explanation of variable abbreviations.

Environmental variable	Excluding soil chemical variables n = 74	Including soil chemical variables n = 38
VAG	.52	.48
ASP	-.43	-.60
LIT	.33	
ALT	.47	.49
SLO	.45	.42
GRZ	-.36	-.35
SAN	.26	.38
NIT		-.42

Table 6. Multiple linear regression models for dependence of relative C₃ grass coverage on environmental variables chosen by forward selection with specified significance ($P < .05$). See Table 2 for explanation of variable abbreviations.

	Independent variables	Regression coefficients (b _i)	Intercept	R ²	F ratio	Significance level of F ratio
A. Excluding soil chemical variables (n = 74)	VAG	3.006		.27	26.4	.000
	ASP	-2.697		.38	21.6	.000
	ALT	0.059		.42	17.2	.000
	SAN	0.323		.46	14.7	.000
			-8.36			
B. Including soil chemical variables (n = 38)	ASP	-4.563		.37	20.6	.001
	NIT	-147.138		.44	14.0	.000
	SLO	2.263		.53	12.5	.000
	VAG	3.121		.60	12.6	.000
			36.15			

cover. Lowest values of SAN and highest values of NIT were recorded from the shale renosterveld communities (Table 1) which also had the lowest relative C₃ grass cover (Table 4).

The results of the regression analysis are shown in Table 6. They indicate the multifactorial nature of sources of variation in the relative C₃ grass cover. The regression model (A) excluding soil chemical variables (n = 74) was only able to account for 46% of the variance while the model (B) including soil data accounted for 60% of the variance. There was a different hierarchy of variables entering the two models. VAG emerged as the strongest independent predictor of C₃ coverage in model A and ASP in model B where VAG ^{was} a poor independent predictor. An analysis of the residuals showed that the assumptions of normality of the residuals were satisfied for both regressions.

GENERAL DISCUSSION

A detailed analysis of the proportional contribution of C₃ and C₄ grass species to the grass flora of the fynbos and allied shrublands in the study area corroborates the findings of a more general study by Vogel et al. (1978). They found that species of both photosynthetic types are equally represented in these communities in the southern and south eastern Cape. Vogel et al. (1978) adduced temperature during the growing season as the single most important factor affecting the distribution of C₃ and C₄ grasses in South Africa. Seasonal process studies in the Humansdorp region by Pierce and Cowling (in preparation) showed that the growth of C₃ and C₄ species was functionally displaced in time. C₃ species grew mainly in the winter months and C₄ species in the summer. This temporal separation of growth activities facilitates the coexistence of both photosynthetic types in a single habitat.

I have shown that C₄ grasses comprise most of the grass cover in all shrubland types (Table 4). Phenological studies by Pierce and Cowling (in preparation) indicated that a few C₄ species (Themeda triandra, Tristachya leucothrix, Sporobolus africana) exhibit (usually weaker) winter growth peaks as well as summer peaks. These bimodal growth patterns may be due to ecotypic variation of physiological characteristics (Tothill 1966, Groves 1975, Downing and Marshall 1980). The dominant grass in all shrubland types in the study area was Themeda triandra, a species renowned for variability in morphology, production and flowering time (Meredith 1955, Downing and Marshall 1980). Summer and winter growth peaks in T. triandra were equally strong (Pierce and Cowling,

in preparation). The ability of this species to exploit winter and summer growing seasons equally well and thus successfully outcompete winter growing C₃ grasses in most habitats, could explain the higher proportional cover of C₄ grasses in the study area. I must stress that the phenological studies by Pierce and Cowling were carried out in level, open "grassland" situations that are not representative of the range of microclimates sampled for this study.

The results of the correlation and regression analyses supported the hypothesis that the relative cover of C₃ grasses would be highest in cool, shaded microclimates. C₃ grasses had highest cover under mature shrubland canopies and on steep poleward slopes at high altitudes. All these sites are indicative of a cooler microclimate, thus favouring the competitive growth of C₃ species, even during the warmer months.

There was no relation between precipitation and the proportional cover of C₃ grasses (cf. Teeri and Stowe 1976, Vogel et al. 1978, Ellis et al. 1979); however the variation in rainfall in the study area (500 – 750mm. yr⁻¹) is not great. This does not imply little variation in soil moisture regime. Slope, aspect, soil texture and soil depth undoubtedly affect the soil moisture of a particular site through the effects of radiation and evapotranspiration (Schulze 1975), and water infiltration and retention (Brady 1974). It cannot be discounted that the higher cover of C₃ grasses on steep poleward slopes was partly attributed to the higher soil moisture levels of these sites (cf. Chazdon 1978, Boutton et al. 1980).

There is some supporting evidence for the hypothesis that a higher relative cover of C₃ grasses would be associated with infertile soils. This relationship could be obscured by the dune sands which had a relatively high cover of C₃ grasses (Table 4) and high levels of nutrients, particularly calcium and phosphorus (Table 1). Dune sands are alkaline (Table 1). Under high pH conditions the availability to plants of certain nutrients, particularly phosphorus, is severely restricted (Brady 1974). It is possible that standard soil analysis techniques do not reveal real amounts of nutrients available for plant assimilation in alkaline, calcareous sands.

Bond (1981) found that C₄ grasses were restricted to fertile soils in the southern Cape mountains where soils are predominantly infertile sands. He argued that deciduous C₄ species are dependent on high nutrient reserves for annual replacement of photosynthetic tissue. Conversely C₃ species, which he claims are mostly evergreen and nutrient conserving, grow in the infertile soils. Leaf longevity in grasses is complex: certainly

the majority of C₃ species in the Humansdorp region exhibit patterns of leaf duration similar to C₄ species (S.M. Pierce, 1982, personal communication).

The fairly low variance accounted for by the regression models indicates the relatively low predictive power of the variables used in the analyses. It is possible that the use of variables that more directly reflect the microclimate (e.g. soil temperature, light penetration) and soil moisture regime would have reduced the unexplained variance in the models.

REFERENCES

- Allen J, Learn J (1973). STEPREG 1: Stepwise linear regression analysis reference manual. Academic Computing Centre, University of Wisconsin, Madison.
- Anon (1942). Weather on the coasts of southern Africa. Vol. 2, part 3. Union of South Africa from Mossel Bay to East London. Government Printer, Pretoria.
- Björkman O (1975). Environmental and biological control of photosynthesis: inaugural address. In: R Marcelle (ed) Environmental and biological control of photosynthesis. Junk, The Hague, pp 1 - 16.
- Black C C (1971). Ecological implications of dividing plants into groups with distinct photosynthetic production capacities. *Adv Ecol Res* 7: 87 - 114.
- Black C C (1973). Photosynthetic carbon fixation in relation to net CO₂ uptake. *Ann Rev Plant Physiol* 24: 253 - 286.
- Bond W J (1981). Vegetation gradients in the southern Cape. M. Sc. Thesis, University of Cape Town, Cape Town.
- Boutton T W, Harrison A T, Smith B N (1980). Distribution of biomass of species differing in photosynthetic pathway along an altitudinal transect in south-eastern Wyoming grassland. *Oecologia (Berl.)* 45: 287 - 298.
- Brady N C (1974). The nature and properties of soils. 8th ed. Macmillan, New York.
- Caldwell M M, Osmond C B, Nott D L (1977). C₄ pathway photosynthesis at low temperature in a cold tolerant Atriplex species. *Plant Physiol* 60: 157 - 164.
- Campbell B M, Cowling R M, Bond W J, Kruger F J (1981). Structural characterization of vegetation in the Fynbos Biome. South African National Scientific Programmes Report No. 52. C S I R, Pretoria.
- Chazdon R (1978). Ecological aspects of the distribution of C₄ grasses in selected habitats of Costa Rica. *Biotropica* 10: 265 - 269.
- Clayton W D (1976). The chorology of African mountain grasses. *Kew Bull* 31: 273 - 288.
- Cowling R M (1982). Syntaxonomic and synecological study of vegetation in the Humansdorp region of the Fynbos Biome. Bothalia (in press).
- Downing B H, Marshall D J (1980). Complementary dominance of Themeda triandra and Panicum maximum examined through shoot production. *Proc Grassld Soc sth Afr* 15: 161 - 171.

- Ehleringer J R (1978). Implications of quantum yield differences in the distributions of C₃ and C₄ grasses. *Oecologia (Berl.)* 31: 255 - 267.
- Ehleringer J R, Björkman O (1977). Quantum yields for CO₂ uptake in C₃ and C₄ plants. *Plant Physiol* 59: 86 - 90.
- Ellis R P (1977). Distribution of the Kranz syndrome in southern African Eragrostoideae and Panicoideae according to bundle sheath anatomy cytology. *Agroplantae* 9: 73 - 110.
- Ellis R P, Vogel J C, Fuls A (1980). Photosynthetic pathways and the geographical distribution of grasses in South West Africa/Namibia. *S Afr J Sci* 76: 307 - 314.
- Evans L T, Wardlaw J F, Williams C N (1964). Environmental control of growth. In: C. Barnard (ed.) *Grasses and grasslands*. Macmillan, London, pp 102 - 125.
- Gibbs Russel G E, Smook L (1980). Name changes of southern African grasses: name changes and additional species since 1955. *Proc Grassld Soc sth Afr* 15: 89 - 97.
- Groves R H (1975). Growth and development of five populations of Themeda australis in response to temperature. *Aust J Bot* 17: 357 - 389.
- Holland P G, Steyn D G, Fuggle R F (1977). Habitat occupation by Aloe ferox Mill. (Liliaceae) in relation to topographic variations in direct beam solar radiation income. *J Biogeogr* 4: 61 - 72.
- Kruger F J (1978). A description of the Fynbos Biome Project. South African National Programmes Report No. 28. C S I R, Pretoria.
- Laetsch W M (1974). The C₄ syndrome: a structural analysis. *Ann Rev Plant Physiol* 25: 27 - 52.
- Lamprechts J J N (1979). Geology, geomorphology and soils. In: Day J, Siegfried W R, Louw G N, Jarman M L (eds). *Fynbos ecology: a preliminary synthesis*. South African National Scientific Programmes Report No. 40: C S I R, Pretoria.
- Meredith D (1955). *The grasses and pastures of South Africa*. C N A, Johannesburg.
- Ode D J, Tieszen L L, Lerman J C (1980). The seasonal contribution of C₃ and C₄ plant species to primary production in a Mixed Prairie. *Ecology* 61 : 1304 - 1311.
- Rice E L, Parenti R L (1978). Causes of decreases in productivity in undisturbed tall grass prairie. *Amer J Bot* 65: 1091 - 1097.

- Roberts B R, Anderson E R , Fourie J H (1975). Veld management recommendation - A reassessment of key species and proper use of factors. Proc. Grassld Soc sth Afr 10: 103 - 109.
- Rundell P W (1980). The ecological distribution of C₄ and C₃ grasses in the Hawaiian Islands. Oecologia (Berl) 45: 354 - 359.
- Scharf H T (1979). Climatic patterns in the southern Cape. Paper presented at the Symposium on Terrestrial Ecology of the Southern Cape. Saasveld Forestry Research Station, George. (unpublished).
- Schulze R E (1975). Incoming radiation on sloping terrain: a general model for use in southern Africa. Agrochemophysika 7: 55 - 61.
- Schulze R E, McGee O S (1978). Climatic indices and classifications in relation to the biogeography of southern Africa. In: Werger M J A (ed) Biogeography and ecology of southern Africa. Junk, The Hague pp 11 - 52.
- Specht R L, Moll E J (1982). Heathlands and sclerophyllous shrublands - an overview. In: Kruger F J, Mitchell D T, Jarvis J U M (eds.) Mediterranean-type ecosystems. The role of nutrients. Springer, Berlin-Heidelberg-New York (in press).
- Taylor H C (1978). Capensis. In: Werger M J A (ed) Biogeography and ecology of southern Africa. Junk, The Hague pp 171 - 229.
- Teeri J A, Stowe L.G (1976). Climatic patterns and distributions of C₄ grasses in North America. Oecologia (Berl.) 23: 1 - 12.
- Tieszen L L, Senyimba M M, Imbamba S K, Troughton J H (1979). The distribution of C₃ and C₄ grasses and carbon isotope discrimination along an altitudinal and moisture gradient in Kenya. Oecologia (Berl.) 37: 337 - 350.
- Tothill J C (1966). Phenological variation in Heteropogon contortus. Aust J Bot 14: 35 - 47.
- Vogel J, Fuls A, Ellis R (1978). The geographic distribution of Kranz grasses in South Africa. S Afr J Sci 74: 209 - 215.
- Weather Bureau (1954). Climate of South Africa. Part 2: Rainfall statistics. Weather Bureau 20, Weather Bureau, Pretoria.

APPENDIX 2

NUMERICAL METHODS OF CLASSIFICATION AND GRADIENT ANALYSIS: A BRIEF OVERVIEW

INTRODUCTION

The high variance of data collected in synecological studies usually necessitates intense sampling. The complex mass of data thus generated must be reduced to a simple form in order to facilitate the interpretation of community patterns and to test and formulate hypotheses regarding plant communities and their relations to environment (Goodall 1970). The development of methods to deal with this problem is conjunct with the growth of the science of plant synecology (see e.g. Whittaker 1962, Goodall 1970, Orloci 1975). The last two decades, particularly, have witnessed a proliferation of mathematically complex multivariate techniques, largely as a result in the improvement of computer facilities and storage capacity.

Methods to study plant communities have developed within the framework of two major (and opposing) hypotheses to explain the basic characteristics of vegetation. The first of these, the community-unit hypothesis, states that vegetation consists of discrete entities which contract each other along narrow boundaries. This hypothesis is embodied in the approach of the classificationists and is stated most explicitly by the Zurich-Montpellier School (Westhoff and van der Maarel 1973, Werger 1974a). On the other hand, the individualistic hypothesis (Gleason 1926) incorporates the principles of species individuality and community continuity. Thus vegetation is visualized as a complex population continuum which is, in general, continuous along environmental gradients (Curtis and McIntosh 1951, Whittaker 1956, 1967, 1973a, McIntosh 1967). This approach has stimulated the development of a variety of techniques which are collectively termed methods of gradient analysis (Whittaker 1967).

At one time a serious controversy raged over which class of techniques is the most appropriate for the study of vegetation. Clearly classification is suitable for a hierarchic systematic approach and essential for vegetation mapping, while gradient analysis is more effective at determining environmental correlates with floristic variation. In the field, vegetation is usually a complex mixture of continuity and discontinuity (Webb 1954, Whittaker 1956, Shimwell 1971, Mueller-Dombois and Ellenberg 1974) and to-day most plant ecologists accept that both approaches, applied to the same data, are complementary in that each reveals a different structure within those data (Anderson 1965, Shimwell 1971, Whittaker 1973a, Noy-Meir and Whittaker 1977).

Both gradient analysis and classificatory methods were used in this study. Below I review briefly the development of methods of both approaches and provide a justification for the techniques employed in the study.

CLASSIFICATION

For the human mind classification is an inherent process and it is therefore no surprise that a classificatory approach was intuitively adopted by the early phytosociological traditions. Of these, the Zurich-Montpellier School has been most successful in producing a formal and systematic classification of plant communities (Whittaker 1973b, Westhoff and van der Maarel 1973, Werger 1974a). The Zurich-Montpellier method is appealing since its final product is an open-ended, hierarchical classification, based on total floristic composition and having diagnostic species for each level of the hierarchy (Werger 1974b). This system permits a comparison of classifications from geographically separated but chorologically related areas as well as the ready incorporation of new *rélevés* into existing classifications. A major criticism of the method is the lack of objectivity both in the choice of stands and the construction of the classification (Poore 1956, Whittaker 1962, Campbell and Moll 1976). Zurich-Montpellier methods have been employed successfully in varied vegetation types in South Africa, including complex and floristically rich Cape fynbos vegetation (e.g. Werger, Kruger and Taylor 1972, McKenzie, Moll and Campbell 1977, Boucher 1978, Glyphis, Moll and Campbell 1978, Laider, Moll, Campbell and Glyphis 1978).

The need for a more objective definition of the association or community-type has resulted in the development of numerous multivariate clustering techniques (see e.g. Williams 1971, Goodall 1973, Orloci 1975). The objectivity of these methods has been questioned, due to the diversity of similarity indexes, clustering algorithms and data transformations which are available for any single method (Walker 1974, Campbell 1978, Bond 1981). Goodall's (1973) statement that "given the same stands and the same data from them, a procedure can be defined which can be applied unequivocally by anyone who understands it, with the assurance that the same result will be obtained" lends credence to the objectivity claims of numerical methods.

Hierarchical numerical classification methods fall into two major categories (Williams and Dale 1965, Williams 1971). (i) Divisive methods which progressively divide the data set versus agglomerative methods which gradually build up clusters. (ii) Monothetic methods in which attributes are considered singly versus polythetic in which a number of different

attributes are considered simultaneously at each step of the classification. Theoretical consideration suggests that divisive methods are preferable to agglomerative ones in that all available information is used at the initial stage; polythetic methods produce fewer 'misclassifications' than monothetic ones as all available information is used at each clustering step (Williams 1971). Thus methods which are both divisive and polythetic should be theoretically optimal.

An early and widely applied monothetic divisive method is association analysis (AA) (Goodall 1953, Williams and Lambert 1959). AA is effective in classifying heterogeneous data, is open-ended, and computationally efficient; at one time AA gained much acceptance as a clustering method. A serious drawback of AA, which explains the general decline in its use, is its tendency to misclassify stands (Taylor 1969, Kruger 1974, Hill, Bunce and Shaw 1975). The development of indicator species analysis (ISA), a polythetic divisive method (Hill et al. 1975, Hill 1979) heralded a major advance in numerical classificatory techniques. ISA produces a classification of stands by the progressive splitting of ordinations (reciprocal averaging) (Hill 1973) at their centres of gravity. At each split indicator (diagnostic) species are chosen to define the two groups of data. ISA has all the advantages of AA and does not produce serious misclassifications (Hill et al. 1975). The technique has proved successful in a variety of vegetation types (Hill et al. 1975, Hall and Swaine 1976, Basset 1978, Daniels 1978, Bond 1981).

A recent improvement of ISA, termed two-way indicator species analysis (TWINSpan) (Hill 1979a), produces a classification of species as well as stands. Furthermore TWINSpan is designed to construct an ordered two-way table which approximates the tabular matrix arrangement of the Zurich-Montpellier School. TWINSpan, therefore, approaches the much desired integration of syntaxonomy with numerical phytosociology (cf. Dale and Webb 1975, Maarel, Orloci and Pignatti 1976, Noy-Meir and Whittaker 1977, Komarkova 1980).

TWINSpan and group average sorting, a polythetic agglomerative clustering method, using relativised Czekanowski coefficient as a similarity index (Campbell and Moll 1976, Campbell 1978, 1980) were used in this study. I used the latter in a first approximation classification of the full data set. Data subsets were classified using TWINSpan which produced good classifications; with some additional manual sorting, two-way phytosociological tables were constructed. This facilitated the systematic approach of the Zurich-Montpellier School through the arrangement synoptic table summarizing regional syntaxonomic relationships.

GRADIENT ANALYSIS

Gradient analysis seeks a clarification of ecological relationships through the arrangement of stands and species importance in relation to actual or derived resource gradients. As such it is a more powerful tool than classification in formulating and testing hypotheses concerning species-environment relationships. Whittaker (1967) recognizes two types of gradient analysis. (i) Direct gradient analysis where samples are arranged in terms of one or more preselected environmental resource gradients. (ii) Indirect gradient analysis (synonymous with ordination) where measurements of sample similarity or species correlation are used to derive abstract axes which may or may not correspond to environmental gradients. These methods seek to demonstrate a continuum rather than a classification although ordinations do indicate the degree of discreteness of nodes and thus aid in the typification of groups (Noy-Meir and Whittaker 1977).

Predictably early methods of direct gradient analysis (Curtis and McIntosh 1951, Whittaker 1956) were developed in North America, in areas of marked topographic relief and little disturbance, where the choice of major resource gradients was no problem (Shimwell 1971, Greig-Smith 1980). Direct gradient analysis has been criticized for permitting bias as to which environmental factors are important and the assumption that simple measures such as elevation, aspect and slope can adequately represent the resource factors affecting vegetation (Austin 1968, Beals 1973). However the assumption implicit in direct gradient analysis, that species importance along resource gradients is distributed according to bell-shaped, Gaussian curves (Whittaker 1956, 1967) links these methods to the hypervolume niche model which affords a sound hypothetical framework (Whittaker 1967, Bond 1981). Coenocline comparisons, an approach which uses two or more community gradients (usually with similar climates) as units of comparison between different landscapes, parent materials and disturbance factors (Whittaker 1973a), has been applied successfully in the mountainous country of the southern and southwestern Cape (Cowling and Campbell 1980, Bond 1981, Midgely and Cowling in prep.).

In most field situations, particularly where topography and climate are uniform and the physical interpretation of floristic gradients is commonly not apparent, indirect gradient techniques are applied. These techniques are termed ordinations and usually operate by reducing the number of dimensions in samples described by presence or quantity of attributes. Recent years have seen an unparalleled growth in the development of ordination techniques and much research has been devoted to their comparative evaluation (Swann 1970, Gauch

and Whittaker 1972a, 1972b, Gauch 1974, Kessel and Whittaker 1976, Robertson 1978, Gauch and Scruggs 1979, Del Moral 1980, Hill and Gauch 1980, Gauch, Whittaker and Singer 1981).

Bray-Curtis or Polar Ordination (PO) (Bray and Curtis 1957, Cottam, Goff and Whittaker 1973) is a mathematically simple technique with an admirable history of successful applications and a good performance record in comparative evaluation studies (Gauch and Whittaker 1972b, Kessel and Whittaker 1976, Gauch et al. 1977). PO makes no assumption regarding the linearity of ecological data and is relatively tolerant of data with a high beta diversity. A major criticism of PO is the subjective selection of stand endpoints (Beals 1973, Cottam et al. 1973, Gauch et al. 1977).

Eigenvector methods are an important class of ordination techniques which are concerned with the distribution of species or samples relative to the axes of greatest variation in the data (Anderson 1971, Shimwell 1971). Factor analysis, one of the earliest of these methods, was introduced to the ecological literature by Goodall (1954). A closely related technique, which is variance rather than covariance oriented, is principle components analysis (PCA) (Orloci 1966, Austin and Orloci 1966); PCA has been extensively used in ecological studies. Unlike PO the axes of PCA are defined objectively.

PCA and allied techniques assume linearity and monotonicity of the relationships among species and between species and environmental gradients (Swan 1970, Austin and Noy-Meir 1971, Beals 1973, Groenewoud 1976, Noy-Meir and Whittaker 1977). There is no general model describing the relationships of species response curves to environmental gradients (Austin 1980) but most studies indicate that response curves are neither linear nor monotonic (Austin 1976, Groenewoud 1976, Westman 1980). As a result ordination axes are distorted, sometimes seriously, so that PCA and related techniques are only effective on data sets of low beta diversity where correlations of species importance and derived gradients are approximately linear (Gauch and Whittaker 1972b, Beals 1973, Gauch 1974, Kessel and Whittaker 1976, Gauch et al. 1977).

The development of reciprocal averaging (RA) (Hill 1973), constitutes an important advance in ordination methodology. Essentially an eigenvector method, RA is relatively tolerant of curvilinearities inherent in ecological data and produces effective ordinations up to a beta diversity of 10 HC (Gauch et al. 1977, Robertson 1978, Del Moral 1980). RA is mathematically akin to PCA but makes no use of compositional distance; it is also related to weighted averages ordination of Whittaker (1956) (Hill 1973). A major

advantage of the method is that it gives both good species and stand ordinations (Hill 1973). Major drawbacks of RA are: (i) the "arch effect" which is a horseshoe-like distortion due to a strong quadratic relation of the second axis to the first; (ii) ecological distances are not preserved, particularly towards the ends of the first axis (Gauch et al. 1977, Hill and Gauch 1980). As a result RA usually does not produce an interpretable second axis.

Hill (1979b, Hill and Gauch 1980) has refined RA to remove these distortions and has called the technique detrended correspondence analysis (DCA). Comparative evaluation studies using simulated and real data indicate that DCA may possibly be the best ordination technique available at present (Hill and Gauch 1980, Gauch et al. 1981). DCA is tolerant of high beta diversity and is scaled in units that can be directly related to beta diversity; the second and higher axes are interpretable and the technique is computationally efficient when compared to other methods (Gauch et al 1981).

In an effort to avoid the problems associated with the curvilinearity of ecological data, non-linear methods have been developed. Gaussian ordination (GO) arranges samples by maximizing the fit of Gaussian curves to the species distributions (Gauch, Chase and Whittaker 1974). Recent studies suggest that Gaussian curves are less common than previously reported (Austin 1976, Westman 1980). GO is tolerant of high beta diversity but is applicable to one-axis coenoclines only and shows no major advantages over RA (Gauch et al. 1981, Westman 1981). Nonmetric ordinations (see Noy-Meir and Whittaker 1977 for a summary) as applied to ecological data (e.g. Anderson 1971, Noy-Meir 1974, Gauch et al. 1981) have yielded some promising results but are still fraught with problems which should be the subject of future research.

The topographic features and vegetation patterns in the Gamtoos valley site were suitable for the application of direct gradient analysis techniques. Peculiarities in the distribution of parent material meant that parallel transects in fynbos (sandy, infertile soils) and thicket-forest (heavier, more fertile soils) could be compared along an elevational gradient (coenocline comparison). This approach was most effective in revealing the response of different vegetation types to similar environmental gradients.

At the lowland site on the Humansdorp peneplain, limited topographic and climatic variation as well as complex disturbance conditions made it virtually impossible to arrange samples in terms of preselected environmental gradients. Clearly, the situation demanded the use of indirect methods and I had the choice of using RA, PO and DCA. I chose the last-mentioned, for reasons stated above. The method produced good ordinations for all

data sets and in all cases ordination axes were significantly correlated with a number of environmental variables. The results of the ordinations are not shown in this thesis - they will be published elsewhere. However the ordinations were used as a check on the discreteness of the communities derived from the classification and to determine the environmental gradients within the various data sets.

REFERENCES

- Anderson D J 1965. Classification and ordination in vegetation science: controversy over a non-existent problem? Journal of Ecology 53, 521 - 526.
- Anderson J B 1971. Ordination methods in ecology. Journal of Ecology 59, 713 - 726
- Austin M P 1968. An ordination study of a chalk grassland community. Journal of Ecology 56, 739 - 758
- Austin M P 1976. On non-linear species response models in ordination. Vegetatio 33, 33 - 41.
- Austin M P 1980. Searching for a model for use in vegetation studies. Vegetatio 42, 11 - 21.
- Austin M P and L Orloci 1966. Geometric models in ecology. 2. An evaluation of some ordination techniques. Journal of Ecology 54, 217 - 227.
- Austin M P and I Noy-Meir 1971. The problem of non-linearity in ordination: experiments with two-gradient models. Journal of Ecology 59, 763 - 773.
- Basset P A 1978. The vegetation of a Camargue pasture. Journal of Ecology 66, 803 - 827.
- Beals E W 1973. Ordination: mathematical elegance and ecological naïveté. Journal of Ecology 61, 23 - 35.
- Bond W 1981. Vegetation gradients in the southern Cape mountains. M.Sc.thesis, University of Cape Town.
- Bray J R and J T Curtis 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27, 217 - 234.
- Campbell B M 1978. Similarity coefficients for classifying relevés. Vegetatio 37, 101 - 109.
- Campbell B M 1980. Some mixed hardwood forest communities of the coastal ranges of southern California. Phytocoenologia 8, 297 - 320.
- Campbell B M and E J Moll 1976. On numerical methods for classifying relevés collected in Braun-Blanquet phytosociological surveys. Journal of South African Botany 42, 45 - 56.
- Cottam G, Goff F G and R H Whittaker 1973. Wisconsin comparative ordination. Ordination and classification of communities. R.H. Whittaker (ed). Junk, The Hague. pp 195 - 221.

- Cowling R M and B M Campbell 1980. Convergence in vegetation structure in the mediterranean communities of California, Chile and South Africa. Vegetatio 43, 191 - 197.
- Curtis J T and R P McIntosh 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32, 476 - 496.
- Dale M B and L J Webb 1975. Numerical methods for the establishment of associations. Vegetatio 30, 77 - 87.
- Daniels R E 1978. Floristic analysis of British mires and mire communities. Journal of Ecology 66, 773 - 802.
- Del Moral R 1980. On selecting indirect ordination methods. Vegetatio 42, 75 - 84.
- Gauch H G 1974. A quantitative evaluation of the Bray-Curtis ordination. Ecology 54, 829 - 836.
- Gauch H G and R H Whittaker 1972a. Coenocline simulation. Ecology 53, 446 - 451.
- Gauch H G and R H Whittaker 1972b. A comparison of ordination techniques. Ecology 53, 868 - 875.
- Gauch H G and W M Scruggs 1979. Variants of Polar Ordination. Vegetatio 40, 147 - 153.
- Gauch H G, Chase G B and R H Whittaker 1974. Ordination of vegetation samples by Gaussian species distributions. Ecology 55, 1382 - 1390.
- Gauch H G, Whittaker R H and T R Wentworth 1977. A comparative study of reciprocal averaging and other ordination techniques. Journal of Ecology 65, 157 - 174.
- Gauch H G, Whittaker R H and S B Singer 1981. A comparative study of nonmetric ordinations. Journal of Ecology 69, 135 - 152.
- Gleason H A 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club 53, 7 - 26.
- Glyphis J, Moll E J and B.M. Campbell 1978. Phytosociological studies on Table Mountain, South Africa: 1. The back table. Journal of South African Botany 44, 281 - 289.
- Goodall D W 1953. Objective methods for the classification of vegetation 1. The use of positive interspecific correlation. Australian Journal of Botany 1, 39 - 63.
- Goodall D W 1954. Objective methods for the classification of vegetation 111. An essay in the use of factor analysis. Australian Journal of Botany 2, 304 - 324.
- Goodall D W 1970. Statistical plant ecology. Annual Review of Ecology and Systematics 1, 99 - 124.

- Goodall D W 1973. Numerical methods of classification. Classification and ordination of communities. R H Whittaker (ed). Junk, The Hague. pp 576 - 615.
- Greig-Smith P 1980. The development of numerical classification and ordination. Vegetatio 42, 1 - 9.
- Groenewoud H van 1976. Theoretical considerations on the covariation of plant species along ecological gradients with regard to multivariate analyses. Journal of Ecology 64, 837 - 847.
- Hall J B and M D Swaine 1976. Classification and ecology of closed-canopy forest in Ghana. Journal of Ecology 64, 913 - 951.
- Hill M O 1973. Reciprocal averaging: an eigenvector method of ordination. Journal of Ecology 61, 237 - 249.
- Hill M O 1979a. TWINSPAN - A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Section of Ecology and Systematics, Cornell University, New York. 48 pp.
- Hill M O 1979b. DECORANA - A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Section of Ecology and Systematics, Cornell University, New York. 30 pp.
- Hill M O and J G Gauch 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42, 47 - 58.
- Hill M O, Bunce R G H and M W Shaw 1975. Indicator species analysis, a divisive polythetic method of classification, and its application to survey of native pinewoods in Scotland. Journal of Ecology 63, 597 - 613.
- Kessel S R and R H Whittaker 1976. Comparisons of three ordination techniques. Vegetatio 32, 21 - 29.
- Komarkova V 1980. Classification and ordination in the Indian Peaks area, Colorado Rocky Mountains. Vegetatio 42, 149 - 163.
- Kruger F J 1974. The physiography and plant communities of the Jakkalsrivier catchment. M.Sc. thesis, University of Stellenbosch.
- Laidler D, Moll E J, Campbell B M and J. Glyphis 1978. Phytosociological studies on Table Mountain, South Africa: 2. The front table. Journal of South African Botany 44, 291 - 295.
- Maarel E van der, Orloci L and S Pignatti 1976. Data-processing in phytosociology, retrospect and anticipation. Vegetatio 32, 65 - 72.

- McIntosh R P 1967. The continuum concept of vegetation. Botanical Review 33, 130 - 187.
- McKenzie B, Moll E J and B M Campbell 1977. A phytosociological study of Orange Kloof, Table Mountain, South Africa. Vegetatio 34, 41 - 53.
- Midgely J M and R M Cowling in prep. A comparison of climatically similar coenoclines in fynbos and karoo-renosterveld near Robertson, Cape Province.
- Mueller-Dombois D and H Ellenberg 1974. Aims and methods of vegetation ecology. John Wiley, New York. 547 pp.
- Noy-Meir I 1974. Catenation: quantitative methods for the definition of coenoclines. Vegetatio 29, 89 - 99.
- Noy-Meir I and R H Whittaker 1977. Continuous multi-variate methods in community analysis: some problems and developments. Vegetatio 33, 79 - 98.
- Orloci L 1966. Geometric models in ecology. 1. The theory and application of some ordination methods. Journal of Ecology 54, 193 - 215.
- Orloci L 1975. Multivariate analysis in vegetation research. Junk, The Hague. 276 pp.
- Poore M E D 1956. The use of phytosociological methods in ecological investigations. Part IV. Journal of Ecology 44, 28 - 50.
- Robertson P A 1978. Comparisons of techniques for ordinating and classifying old growth flood-plain forests in southern Illinois. Vegetatio 37, 43 - 51.
- Shimwell D W 1971. Description and classification of vegetation. Sidgwick and Jackson, London. 322 pp.
- Swan J M A 1970. An examination of some ordination problems by use of simulated vegetational data. Ecology 51, 89 - 102.
- Taylor H C 1979. A vegetation survey of the Cape of Good Hope Nature Reserve. M.Sc. thesis, University of Cape Town.
- Walker B H 1974. Some problems arising from the preliminary manipulation of plant ecological data for subsequent numerical analyses. Journal of South African Botany 40, 1 - 13.
- Webb D A 1954. Is the classification of plant communities either possible or desirable. Botaniska Tidsskrifte 51, 362 - 370.
- Werger M J A 1974a. On concepts and techniques applied to the Zurich-Montpellier method of vegetation survey. Bothalia 11, 309 - 323.

- Werger M J A 1974b. The place of the Zurich-Montpellier method in vegetation science. Folia Geobot Phytotax 9, 99 - 109.
- Westhoff V and E van der Maarel 1973. The Braun-Blanquet approach. Ordination and classification of communities. R H Whittaker (ed.) : Junk, The Hague. pp 617 - 726.
- Westman W E 1980. Gaussian analysis: identifying environmental factors influencing bell-shaped species distribution. Ecology 61, 733 - 739.
- Westman W E 1981. Factors influencing the distribution of species of California coastal sage scrub. Ecology 62, 439 - 455.
- Whittaker R H 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs 26, 1 - 80.
- Whittaker R H 1962. Classification of natural communities. Botanical Review 28, 1 - 239.
- Whittaker R H 1967. Gradient analysis of vegetation. Biological Review 49, 207 - 264.
- Whittaker R H 1973a. Direct gradient analysis: techniques and results. Ordination and classification of communities. R H Whittaker (ed). Junk, The Hague. pp 7-51.
- Whittaker R H 1973b. Approaches to classifying vegetation. Ordination and classification of communities. R H Whittaker (ed). Junk, The Hague. pp. 193 - 222.
- Williams W T 1971. Principles of clustering. Annual Review of Ecology and Systematics 2, 303 - 326.
- Williams W T and M B Dale 1965. Fundamental problems in numerical taxonomy. Advances in Botanical Research 2, 35 - 68.
- Williams W T and J M Lambert 1959. Multivariate methods in plant ecology. 1. Association-analysis in plant communities. Journal of Ecology 47, 83 - 101.

APPENDIX 3

CHECK LIST AND GEOGRAPHICAL DISTRIBUTION OF TAXA

Appendix 3. Check list of the Humansdorp sample flora and geographical distribution of the taxa. For explanation of abbreviations see Paper 2.

PTERIDOPHYTA

Phytochorological group

<u>Asplenium adiantum nigrum</u> L.	ATL
<u>A. erectum</u> Bory ex Willd.	AEN
<u>A. lunulatum</u> Sw.	AEN
<u>A. rutaefolium</u> (Berg.) Kuntze	AEN
<u>A. splendens</u> Kunze	AEN
<u>Blechnum attenuatum</u> Sw. (Mett.)	AEN
<u>Ceterach cordatum</u> (Thunb.) Desv.	AEN
<u>Cheilanthes bergiana</u> Schlecht. ex Kunze	AEN
<u>C. contracta</u> (Fée) Mett. ex Kuhn	KEN
<u>C. multifida</u> Sw.	AEN
<u>Dryopteris inaequalis</u> (Schlecht dl) O. Kze.	AEN
<u>Mohria caffrorum</u> (L.) Desv.	CAL
<u>Pellaea viridis</u> (Forsk.) Prantl	AEN
<u>Pteridium aquilinum</u> (L.) Kuhn	WID
<u>Schizaea pectinata</u> (L.) Swartz	CAL

GYMNOSPERMAE

CUPRESSACEAE

<u>Widdringtonia nodiflora</u> (L.) Powrie	CAL
--	-----

PODOCARPACEAE

<u>Podocarpus falcatus</u> R. Br.	AEN
<u>P. latifolius</u> (Thunb.) R. Br.	AEN

ANGIOSPERMAE: MONOCOTLEDONEAE

AMARYLLIDACEAE

<u>Boophane disticha</u> Herb.	TRW	
<u>Brunsvigia gregaria</u> R.A. Dyer	CKL	endemic 1
<u>Brunsvigia litoralis</u> R.A. Dyer	CEN	endemic
<u>Cyrtanthus affinis</u> R.A. Dyer	CEN	endemic
<u>C. helictus</u> Lebm.	TEN	
<u>Scadoxys puniceus</u> (L.) Friis & Nordal	ATP	

COMMELINACEAE

<u>Commelina africana</u> L.	WID
<u>C. benghalensis</u> L.	WID
<u>Cyanotis speciosa</u> (L.f.) Hassk.	WID

CYPERACEAE

<u>Bulbostylis collinum</u> (Kunth.) C.B.Cl.	AEN
<u>B. humilis</u> Kunth.	AEN
<u>Cyperus albostriatus</u> Schrad.	AEN
<u>Ficinia acuminata</u> (Steud.) Nees	CEN

<u>F. albicans</u> Nees	CEN	
<u>F. aphylla</u> Nees	CEN	
<u>F. bulbosa</u> (L.) Nees	CEN	
<u>F. filiformis</u> (Lam.) Schrad.	CEN	
<u>F. gracilis</u> Schrad.	CAL	
<u>F. indica</u> (Lam.) Pfeiff.	CEN	
<u>F. involuta</u> Nees	CEN	
<u>F. lateralis</u> (Vahl.) Kunth	CEN	
<u>F. leiocarpa</u> Nees	AEN	
<u>F. nigrescens</u> (Schrad.) J. Raynell	CEN	
<u>F. ramosissima</u> Kunth	CEN	
<u>F. stolonifera</u> Boeck.	CAL	
<u>F. tribracteata</u> Boeck.	CEN	
<u>F. tristachya</u> (Rottb.) Nees	CEN	
<u>Fuirena hirsuta</u> (Berg.) P.L. Forbes	CAL	
<u>Kyllinga alba</u> Nees	WID	
<u>Pycnus</u> cf. <u>tanceus</u> (Thunb.) Turril		
<u>Schoenoxiphium caricoides</u> C.B. Cl.	AEN	
<u>S. sparteum</u> (Wahlenb.) Kük.	AEN	
<u>Scirpus antarcticus</u> L.	CEN	
<u>S. venustulus</u> (Kunth) Boeck.	CEN	
<u>Tetraria capillacea</u> C.B.Cl.	CEN	
<u>T. circinalis</u> C.B.Cl.	CEN	
<u>T. compar</u> (L.) Lestib.	CEN	
<u>T. compressa</u> Turril.	CEN	
<u>T. cuspidata</u> (Rottb.) C.B.Cl.	CAL	
<u>T. involucreta</u> C.B.Cl.	CEN	
<u>T. pleiosticha</u> C.B.Cl.	CEN	
<u>T. robusta</u> (Kunth) C.B.Cl.	CEN	endemic
<u>T. secans</u> C.B.Cl.	CEN	
<u>T. sp.</u>		
<u>T. sp.</u>		

DIOSCORACEAE

<u>Dioscorea sylvatica</u> (Kunth) Eckl.	AEN	
--	-----	--

HAEMADORACEAE

<u>Cyanella lutea</u> L.f.	KEN	
<u>Lanaria lanata</u> (L.) Friis & Nordal	CEN	
<u>Wachendorfia paniculata</u> L.	CEN	
<u>W. thyrsiflora</u> L.	CEN	

HYPOXIDACEAE

<u>Hypoxis longifolia</u>	CEN	
<u>H. obliqua</u> Jacq.	CEN	
<u>H. sobolifera</u> Jacq.	CAL	
<u>H. stellipilis</u> Ker	CKN	endemic
<u>H. zeyheri</u> Bak.	CEN	endemic
<u>H. sp.</u>		
<u>Spiloxene minuta</u> (L.) Fourc.	CEN	
<u>S. sp.</u>		

IRIDACEAE

<u>Anapalina caffra</u> (Bak.) Lewis	CEN	
<u>A. intermedia</u> (Bak.) Lewis	CEN	endemic
<u>A. nervosa</u> (Thunb.) Lewis	CEN	
<u>Aristea anceps</u> Eckl.	CEN	
<u>A. pusilla</u> (Thunb.) Ker ssp. <u>pusilla</u>	CEN	
<u>Babiana patersoniae</u> L.	CEN	
<u>B. sambucina</u> (Jacq.) Ker	CKL	
<u>Bobartia orientalis</u> Gillet	CEN	endemic
<u>Chasmanthe aethiopica</u> (L.) N.E.Br.	CEN	
<u>Dierama pendulum</u> (L.f.) Bak.	AEN	
<u>Dietes iridioides</u> (L.) Sweet ex Klatt.	ATL	
<u>Geissorhiza bracteata</u> Klatt.	CEN	
<u>Gladiolus floribundus</u> Jacq. ssp. <u>floribundus</u>	CEN	
<u>G. guenzii</u> Kunze	CTL	
<u>G. liliaceus</u> Houtt.	CEN	
<u>G. longicollis</u> Bak.	CAL	
<u>G. permeabilis</u> Delaroche	CEN	
<u>G. sp.</u>		
<u>Hesperantha angusta</u> (Willd.) Ker		
<u>H. falcata</u> Ker-Gawl.	CEN	
<u>Hexaglottis longifolia</u> Vent.	CEN	
<u>Homoglossum huttonii</u> N.E.Br.	CEN	endemic
<u>Ixia orientalis</u> Ker	CEN	endemic
<u>Melasphaerula ramosa</u> (L.) N.E.Br.	WID	
<u>Micranthus plantagineus</u> Eckl.	CEN	
<u>Moraea algoensis</u> Goldbl.	CEN	endemic
<u>M. polystacha</u> (Thunb.) Ker	KEN	
<u>Romulea atrandra</u> G.J. Lewis	CEN	
<u>R. dichotoma</u> (Thunb.) Bak.	CEN	
<u>R. longipes</u> Schltr.	CEN	endemic
<u>R. rosea</u> (L.) Eckl.	CEN	
<u>Tritonia lineata</u> Ker.	CAL	
<u>Watsonia humilis</u> Mill.	CEN	
<u>W. longifolia</u> Matthews ex L. Bol.	CEN	endemic
<u>W. meriana</u> Mill.	CAL	
<u>W. pillansii</u> L.Bol.	CEN	

LILIACEAE

<u>Albuca minor</u> L.	CEN	
<u>Aloe africana</u> Mill.	TEN	endemic
<u>A. arborescens</u> Mill.	ATL	
<u>A. ferox</u> Mill.	TKL	
<u>A. microcantha</u> Haw.	CTL	endemic
<u>A. pluridens</u> Haw.	TEN	
<u>A. saponaria</u> (Ait.) Haw.	ATP	
<u>Androcymbium albanense</u> Schönl.	CEN	endemic
<u>A. capense</u> (L.) Krause	CKL	

<u>Asparagus aethiopicus</u> L.	WID	
<u>A. africanus</u> Lam.	WID	
<u>A. asparagoides</u> (L.) Wright	WID	
<u>A. capensis</u> L.	CKL	
<u>A. crassifolius</u> Jessop	TKL	endemic
<u>A. densiflorus</u> (Kunth) Jessop	TEN	
<u>A. krebsiana</u> (Kunth) Jessop	TZL	
<u>A. macowanii</u> Bak.	AEN	
<u>A. mucronatus</u> Jessop	KEN	
<u>A. racemosus</u> Willd.	TKL	
<u>A. scandens</u> Thunb.	AEN	
<u>A. setaceus</u> (Kunth) Jessop	AEN	
<u>A. striatus</u> (L.f.) Thunb.	KEN	
<u>A. suaveolens</u> Burch.	WID	
<u>A. subulatus</u> Thunb.	ATL	
<u>A. thunbergianus</u> Schult.	CEN	
<u>Behnia reticulata</u> (Thunb.) Didr.	ATL	
<u>Bulbine alooides</u> Willd.	TKL	
<u>B. caulescens</u> L.	TKL	endemic
<u>B. narcissifolia</u> Salm-Dyck	AEN	
<u>Chlorophytum comosum</u> (Thunb.) Jacq.	AEN	
<u>C. crispum</u> (Thunb.) Bak.	CKL	
<u>C. sp.</u>		
<u>Drimia elata</u> Jacq.	WID	
<u>D. haworthoides</u> Bak.	TKL	endemic
<u>Eriospermum brevipes</u> Bak.	CEN	endemic
<u>E. cordiforme</u> Salter	CEN	endemic
<u>E. dregei</u> Schönl.	CKL	endemic
<u>E. porphyrium</u> Archibald	CEN	endemic
<u>E. sp.</u>		
<u>E. sp.</u>		
<u>Gasteria armstrongii</u> Schoenl.	CKL	endemic
<u>G. croucheri</u> (Hook.f.) Bak.	TKL	endemic
<u>G. sp.</u>		
<u>Haworthia fasciata</u> (Willd.) Haw.	KEN	endemic
<u>H. radula</u> (Jacq.) Haw.	KEN	endemic
<u>Lachenalia algoensis</u>	CEN	endemic
<u>Ledebouria cooperi</u> (Hook.f.) Jessop	TRW	
<u>L. revoluta</u> (L.f.) Jessop	TRW	
<u>L. socialis</u> (Bak.) Jessop	TKL	endemic
<u>L. undulata</u> (Jacq.) Jess.	WID	
<u>L. sp.</u>		
<u>L. sp.</u>		
<u>Massonia pustulata</u> Jacq.	CKL	
<u>Ornithogalum miniatum</u> Jacq.	CKL	
<u>O. sp.</u>		
<u>O. sp.</u>		
<u>O. sp.</u>		
<u>O. sp.</u>		

<u>Polyxena ensifolia</u> Schönl.	CKL
<u>Trachyandra affinis</u> Kunth	CTL
<u>T. ciliata</u> (L.f.) Kunth	CKL
<u>Tulbaghia violaceae</u> Harv.	CEN
<u>Sansiviera</u> sp.	

ORCHIDACEAE

<u>Acrolophia capense</u> (Berg) Fourcade	CEN	
<u>A. micrantha</u> (Lindl.) Schlecht. & Bolus	CEN	
<u>Bartholina ethelae</u> Bolus	CEN	
<u>B. sp.</u>		
<u>Bonatea speciosa</u> Willd.	ATL	
<u>Brachychortis macowaniana</u> Reichb.f.	CEN	
<u>Cytorchis arcuata</u> (Lindl.) Schlecht.	AEN	
<u>Disa</u> sp.		
<u>Holothrix</u> cf. <u>lindleyana</u> Reichb. f.		
<u>Satyrium coriifolium</u> Sw.	CEN	
<u>S. membranaceum</u> Sw.	CAL	
<u>S. princeps</u> Bol.	CEN	endemic

POACEAE

<u>Aristida junciformis</u> Trin. et Rupr.	ATL	
<u>Brachiaria serrata</u> (Spreng.) Stapf.	TRW	
<u>Briza maxima</u> L.	WID *	
<u>B. minor</u> L.	WID *	
<u>Bromus japonicus</u> Thunb.	WID *	
<u>Cynodon dactylon</u> (L.) Pers.	WID	
<u>Cymbopogon marginatus</u> (Steud.) Stapf.	TRW	
<u>Digitaria eriantha</u> Steud. subsp. <u>eriantha</u>	TRW	
<u>Diheteropon filifolius</u> (Nees) Clayton	AEN	
<u>Ehrharta calycina</u> Sm.	WID	
<u>E. capensis</u> Thunb.	CEN	
<u>E. erecta</u> Lam.	WID	
<u>E. ramosa</u> Thunb.		
<u>E. villosa</u> Schult f.	CKL	
<u>Eragrostis capensis</u> (Thunb.) Trin.	TRW	
<u>E. curvula</u> (Schrud.) Nees	WID	
<u>E. obtusa</u> Munro ex Fic. et Hiern	KZL	
<u>Eustachys paspaloides</u> (Vahl.) Lanza et Mattei	TRW	
<u>Festuca caprina</u> Nees	AEN	
<u>F. costata</u> Nees	AEN	
<u>F. scabra</u> Vahl	AEN	
<u>Harpochoa falx</u> Kunth.	AEN	
<u>Helictotrichon hirtulum</u> (Steud.) Schweick.	CAL	
<u>Heteropogon contortus</u> (L.) Beauv.	TRW	
<u>Imperata cylindrica</u> (L.) Beauv.	WID	
<u>Karoochloa curva</u> (Nees) Conert & Turpe	CKL	
<u>Koelaria capensis</u> (Steud.) Nees	CAL	

<u>Lasiochloa longifolia</u> (Schrad.) Kunth	CEN	
<u>L. obtusifolia</u> Nees	CEN	
<u>Melica decumbens</u> Thunb.	AEN	
<u>M. racemosa</u> Thunb.	CAL	
<u>Merxmuellera disticha</u> (Nees) Conert	AEN	
<u>M. stricta</u> (Schrad.) Conert	CAL	
<u>Oplismenus hirtellus</u> (L.) Beauv.	ATL	
<u>Panicum deustum</u> Thunb.	TRW	
<u>P. maximum</u> Jacq.	TRW	
<u>P. natalense</u> Hochst.	AEN	
<u>P. obumbratum</u> Stapf	TEN	endemic
<u>Pentaschistis airoides</u> (Nees) Stapf	CKL	
<u>P. angustifolia</u> (Nees) Stapf	CAL	
<u>P. curvifolia</u> (Schrad.) Stapf	CEN	
<u>P. eriostoma</u> (Nees) Stapf	CEN	
<u>P. heptamera</u> (Nees) Stapf	CEN	endemic
<u>P. involuta</u> (Steud.) Adamson	CEN	
<u>P. tortuosa</u> (Trin.) Stapf	CEN	
<u>Plagiochloa uniola</u> (L.f.) Adamson & Sprague	CEN	
<u>Rhynchelytrum setifolium</u> (Stapf) Chiov.	TRW	
<u>Setaria flabellata</u> Stapf	TRW	
<u>Sporobolus africanus</u> (Poir.) Robyns & Tournay	TRW	
<u>S. fimbriatus</u> Nees	TRW	
<u>S. cf. pectinatus</u> Hack.		
<u>S. schlechteri</u> Schweick.	AEN	
<u>Stipa dregeana</u> Steud	AEN	
<u>Stipagrostis zeyheri</u> (Nees) De Wint. subsp. <u>zeyheri</u>	CEN	
<u>Stenotaphrum secundatum</u> (Walt) O. Ktze	TEN	
<u>Themeda triandra</u> Forsk.	TRW	
<u>Trachypogon spicatus</u> (L.f.) O. Ktze	AEN	
<u>Triraphis</u> sp.		
<u>Tristachya leucothrix</u> Nees	TRW	
<u>Vulpiabromoides</u> (L.) S.F. Gray	WID	*

RESTIONACEAE

<u>Cannamois virgata</u> (Rottb.) Steud.	CEN
<u>Chondropetalum microcarpum</u> (Kunth) Pillans	CEN
<u>Elegia fistulosa</u> Kunth	CEN
<u>E. parviflora</u> Kunth	CEN
<u>E. vaginulata</u> Mast.	CEN
<u>Hypodiscus albo-aristatus</u> (Nees) Mast.	CEN
<u>H. aristatus</u> (Thunb.) Nees	CEN
<u>H. striatus</u> (Kunth) Mast.	CEN
<u>H. synchroolepis</u> (Steud.) Mast.	CEN
<u>H. willdenowia</u> (Nees) Mast.	CEN
<u>Restio compressus</u> Rottb.	CEN
<u>R. cuspidatus</u> Thunb.	CEN
<u>R. eleocharis</u> Nees	CEN
<u>R. fruticosus</u> Thunb.	CEN
<u>R. leptocladus</u> Mast.	CEN
<u>R. papillosa</u> (undescribed)	CEN

<u>R. sieberi</u> Mast.	CAL	
<u>R. triticeus</u> Rottb.	CEN	
<u>Thamnochortus argenteus</u> Kunth	CEN	
<u>T. fruticosus</u> Berg.	CEN	
<u>T. glaber</u> Pillans	CEN	e ndemic
<u>T. insignis</u> Mast.	CEN	

ANGIOSPERMAE: DICOTYLEDONAE

ACANTHACEAE

<u>Barleria obtusa</u> Nees	KZL	
<u>B. pungens</u> L.f.	CKL	
<u>Blepharis capensis</u> (L.f.) Pers	KEN	
<u>B. integrifolia</u> (L.f.) E. Mey	TRW	
<u>B. procumbens</u> (L.f.) Pers	CKL	endemic
<u>Chaetacanthus setiger</u> (Pers.) Lind.	CTL	
<u>Hypoestes aristata</u> (Vahl) R. Br.	TRW	
<u>H. verticillaris</u> (L.f.) R. Br.	TRW	
<u>Isoglossa eckloniana</u> (Nees) Lind.	ATL	
<u>Justica acuta</u> (C.B.Cl.)	CKL	endemic
<u>Thunbergia capensis</u> Retz.	CKL	

AIZOACEAE

<u>Aizoon glinoides</u> L.f.	CKL	
<u>A. rigidum</u> L.f.	CKL	
<u>Aptenia cordifolia</u> (L.) Schw.	TKL	
<u>Carpobrotus deliciosus</u> (L. Bol.) L. Bol.	CKN	
<u>C. edulis</u> (L.) N.E.Br.	CKN	
<u>Delosperma echinatum</u> (Ait.) Schw.	KEN	endemic
<u>D. ecklonis</u> (Salm-Dyck) Schw.	TKL	endemic
<u>D. litorale</u> L. Bol.	CEN	
<u>D. sp.</u>		
<u>Drosanthemum floribundum</u> (Haw.) Schw.	KEN	
<u>D. gracillimum</u> L. Bol.	KEN	
<u>D. intermedium</u> L. Bol.	CKL	endemic
<u>D. liguae</u> (N.E.Br.) Schw.	TKL	endemic
<u>Glottiphyllum longum</u> (Haw.) N.E.Br.	TKL	e ndemic
<u>Lampranthus dependens</u> (L. Bol.) N.E.Br.	CKL	
<u>L. elegans</u> (Jacq.) N.E.Br.	CKL	
<u>L. pauciflorus</u> (L. Bol.) N.E.Br.	CKL	
<u>L. productus</u> (Haw.) N.E.Br.	CKL	endemic
<u>L. spectabilis</u> (Haw.) N.E.Br.	CKL	endemic
<u>Mesembryanthemum aitonis</u> Jacq.	CKL	
<u>Pharnaceum incanum</u> L.	CEN	
<u>Ruschia congesta</u> (Haw.) L. Bol.	CKL	
<u>R. tenella</u> (Haw.) Schw.	CKL	
<u>R. sp.</u>		
<u>Tetragonia fruticosa</u> L.	TKL	
<u>Trichodiadema decorum</u> (N.E.Br.) Stearn	TKL	endemic

ANACARDIACEAE

<u>Harpephyllum caffrum</u> Bernh	TEN
<u>Laurophyllus capensis</u> Thunb.	AEN
<u>Rhus chirindensis</u> E.G. Baker	ATL
<u>R. crenata</u> Thunb.	CTL
<u>R. dentata</u> Thunb.	WID
<u>R. fastigata</u> Eckl. & Zeyh.	AEN
<u>R. glauca</u> Thunb.	CTL
<u>R. incisa</u> L.f.	CTL
<u>R. laevigata</u> L.	CAL
<u>R. longispina</u> Eckl. & Zeyh.	CTL
<u>R. lucida</u> L.	ATL
<u>R. macowanii</u> Schoenl.	ATL
<u>R. refracta</u> Eckl. & Zeyh.	TEN
<u>R. rosmarinifolia</u> Vahl.	CEN
<u>R. schlechteri</u> Diels	CTL

APOCYNACEAE

<u>Acokanthera oppisitifolia</u> (Lam.) Codd	ATL
<u>Carissa bispinosa</u> (L.) Desf. ex Brenan	TRW
<u>C. haematocarpa</u> (Eckl.) A.DC.	TKL
<u>Gonioma kamassi</u> E. Meyer	AEN
<u>Pachypodium bispinosum</u> (L.f.) A.DC.	KEN

ARALIACEAE

<u>Cussonia gamtooensis</u> Strey	TEN	endemic
<u>C. spicata</u> Thunb.	ATL	
<u>C. thyrsoiflora</u> Thunb.	CTL	

ASCLEPIADACEAE

<u>Asclepias physocarpa</u> Schltr.	WID
<u>Astephanus marginatus</u> Decne.	TEN
<u>Ceropegia carnosa</u> E. Mey.	TEN
<u>Cynanchum ellipticum</u> (Harv.) R.A. Dyer	ATL
<u>C. obtusifolium</u> L.f.	ATL
<u>C. natalitium</u> Schltr.	TEN
<u>Fockea edulis</u> (Thunb.) K. Schum.	TKL
<u>Microlooma tenuifolia</u> K. Schum.	CEN
<u>Sarcostemma viminalis</u> (L.) R. Br.	TKL
<u>Schizoglossum cordifolium</u> E. Mey.	CAL
<u>Secamone alpini</u> Schultes	ATL
<u>S. frutescens</u> (E. Mey.) Decne	TEN
<u>Tylophora cordata</u> (Thunb.) Druce	ATL

BORAGINACEAE

<u>Anchusa capensis</u> Thunb.	WID
<u>Cynoglossum hispidum</u> Thunb.	CKL
<u>Ehretia rigida</u> (Thunb.) Druce	TRW
<u>Lobostemon argenteus</u> Bueck.	CEN

BRUNIACEAE

<u>Berzelia intermedia</u> Schlecht.	CEN
<u>Brunia nodiflora</u> L.	CEN

CAMPANULACEAE

<u>Cyphia heterophylla</u> Presl.	WID
<u>C. sp.</u>	
<u>Lightfootia cinerea</u> (L.f.) Sond.	CEN
<u>L. divaricata</u> Buek.	CTL
<u>L. rubens</u> Buek.	CEN
<u>Lobelia erinus</u> L.	WID
<u>L. scabra</u> Thunb.	CAL
<u>L. tomentosa</u> L.f.	CEN
<u>L. sp.</u>	
<u>L. sp.</u>	
<u>Prismatocarpus strictus</u> A.DC.	CEN

CAPPARACEAE

<u>Capparis sepiaria</u> L.	TZL
<u>Maerua cafra</u> (DC.) Pax	TZL
<u>M. racemulosa</u> (DC.) Gilg & A. Benn.	TEN

CARYOPHYLLACEAE

<u>Cerastium capense</u> Sond.	CAL
<u>Silene bellidioides</u> Sond.	CEN
<u>S. burchellii</u> Otth.	WID
<u>S. gallica</u> L.	WID *
<u>S. primulaeflora</u> Eckl. & Zeyh.	CEN endemic
<u>Spergularia cf. marginata</u> (DC.) Kitt	

CELASTRACEAE

<u>Cassine aethiopica</u> Thunb.	TRW
<u>C. crocea</u> (Thunb.) O. Ktze	ATL
<u>C. maritima</u> (Bol.) L. Bol.	CTL
<u>C. peragua</u> L.	ATL
<u>C. reticulata</u> (Eckl. & Zeyh.) Codd	TEN endemic
<u>C. tetragona</u> (L.f.) Loes.	ATL
<u>Maytenus acuminatus</u> (L.f.) Loes.	AEN
<u>M. heterophylla</u> (Eckl. & Zeyh.) N. Robson	TRW
<u>M. nemorosa</u> (Eckl. & Zeyh.) Marais	ATL
<u>M. oleoides</u> (Lam.) Loes	CEN
<u>M. procumbens</u> (L.f.) Loes	TEN
<u>M. undata</u> (Thunb.) Blakelock	ATL
<u>Pterocelastrus tricuspidatus</u> (Lam.) Sond.	ATL
<u>Putterlickia pyracantha</u> (L.) Szyszyl.	TRW

COMPOSITAE

<u>Arctotis arctoides</u> (L.f.) O. Hoffman	CAL	
<u>Aster bakeranus</u> (Burt Davy) C.A. Smith	WID	
<u>Athanasia dentata</u> L.	CEN	
<u>A. punctata</u> (DC.) Harv.	CAL	
<u>Athrixia crinata</u> (L.) Druce	CEN	
<u>Berkheya angustifolia</u> (Houtt.) Merril	CEN	
<u>B. carduoides</u> (Less.) Hutch.	CAL	
<u>B. heterophylla</u> (Thunb.) O. Hoffm.	CAL	
<u>Brachylaena glabra</u> (L.f.) Druce	ATL	
<u>B. ilicifolia</u> (Lam.) Phill. & Schweick.	TEN	
<u>Chrysanthemoides monolifera</u> (L.) Norl.	CAL	
<u>Chrysocoma tenuifolia</u> Berg.	KEN	
<u>Cineraria lobata</u> L' Her.	WID	
<u>Corymbium africanum</u> L.	CEN	
<u>C. latifolium</u> Harv.	CEN	endemic
<u>Cotula sericea</u> L.f.	CEN	
<u>C. turbinata</u> L.	WID	
<u>Cullumia decurrens</u> Less.	CEN	
<u>C. setosa</u> (L.) R.Br.	CEN	
<u>Diplopappus laevigatus</u> Sond.	CEN	endemic
<u>Disparago ericoides</u> Gaertn.	CAL	
<u>Elytropappus rhinocerotis</u> (L.f.) Less.	CKL	
<u>Eriocephalus africanus</u> L.	CKL	
<u>Euryops algoensis</u> DC.	CEN	
<u>E. brevipapposus</u> M.O.Hend.	ATL	
<u>E. euryopoides</u> (DC.) B. Nordenstram	CTL	endemic
<u>E. munitus</u> (L.f.) B. Nordenstram	CEN	endemic
<u>E. spathaceus</u> DC.	CKL	
<u>E. ursinoides</u> B. Nord.	CEN	endemic
<u>Eroeda imbricata</u> (Lam.) Levyns	CEN	
<u>E. intermedia</u> DC. Levyns	CEN	endemic
<u>Felicia amoena</u> (Sch. Bip.) Levyns ssp. <u>latifolia</u> Grau	CEN	
<u>F. echinata</u> (Thunb.) Nees	CEN	endemic
<u>F. fascicularis</u> DC.	KEN	
<u>F. filifolia</u> (Vent.) Burt Davy ssp. <u>filifolia</u>	KEN	
<u>F. zeyheri</u> (Less.) Nees ssp. <u>zeyheri</u>	CKL	endemic
<u>Gazania krebsiana</u> Less. ssp. <u>krebsiana</u>	WID	
<u>G. linearis</u> (Thunb.) Druce	ATL	
<u>Gerbera ambigua</u> (Cass.) Sch. Bip.	WID	
<u>G. cordata</u> (Thunb.) Less.	AEN	endemic
<u>Gnaphalium repens</u> L.	CEN	
<u>Haplocarpha lyrata</u> Harv.	CEN	endemic
<u>H. scaposa</u> Harv.	CAL	
<u>Helichrysom anomalum</u> Less.	CAL	
<u>H. appendiculatum</u> (L.f.) Less.	CAL	
<u>H. asperum</u> (Thunb.) Hilliard & Burt	WID	
<u>H. aureum</u> (Houtt.) Merril	CAL	
<u>H. capillacum</u> (Th.) Less	WID	
<u>H. cymosum</u> (L.) D. Don	CAL	

<u>H. felinum</u> (Thunb.) Less.	CAL	
<u>H. herbaceum</u> (Andr.) Sweet	CAL	
<u>H. nudifolium</u> (L.) Less.	CAL	
<u>H. odoratissimum</u> (L.) Less	CAL	
<u>H. paniculatum</u> (L.) Willd.	CEN	
<u>H. rosum</u> (Berg.) Less.	CKL	
<u>H. striatum</u> Thunb.	CEN	endemic
<u>H. subglomeratum</u> Less.	CEN	endemic
<u>H. teretifolium</u> (L.) D. Don	CTL	
<u>H. vellereum</u> R.A. Dyer	CEN	endemic
<u>H. zeyheri</u> Less.	KEN	
<u>Hypochoeris radicata</u> L.	WID *	
<u>Leontonyx glomeratus</u> (L.) DC.	CEN	
<u>Metalasia aurea</u> D. Don	CEN	endemic
<u>M. gnaphaloides</u> (Thunb.) Druce	CEN	
<u>M. muricata</u> (L.) R.Br.	CAL	
<u>Mikania cordata</u> (Burm.f.) B.L. Robinson	TRW	
<u>Osteospermum imbricatum</u> L.	CTL	
<u>O. junceum</u> Berg.	CEN	
<u>Othonna carnosae</u> Less.	CTL	
<u>O. rufibarbis</u> Harv.	CEN	endemic
<u>Piloselloides hirsuta</u> (Forskl.) Jeffrey	WID	
<u>Pteronia incana</u> (Burm.) DC	CKL	
<u>P. teretifolia</u> (Thunb.) Fourc.	CEN	endemic
<u>Relbunium calycinum</u> (L.f.) L'Herit ssp. <u>lanceolata</u> Bremer	CEN	endemic
<u>R. genistaefolia</u> (L.) L'Herit	CKL	
<u>R. pungens</u> L'Her. ssp. <u>pungens</u>	CEN	
<u>Senecio albanensis</u> DC.	CTL	
<u>S. angulatus</u> L.f.	ATL	
<u>S. articulata</u> (L.) Haw.	KEN	
<u>S. burchellii</u> DC.	WID	
<u>S. chrysocoma</u> Meerburgh	CAL	
<u>S. crenatus</u> Thunb.	CEN	endemic
<u>S. deltoideus</u> Less.	AEN	
<u>S. elegans</u> L.	CEN	
<u>S. erubescens</u> Ait.	CAL	
<u>S. ilicifolius</u> Thunb.	CEN	
<u>S. longifolius</u> L.	CTL	
<u>S. macroglossus</u> DC.	TEN	
<u>S. mikanooides</u> Otto ex Harv.	AEN	
<u>S. oederiaefolius</u> DC.	CEN	
<u>S. oliganthus</u> DC.	CEN	
<u>S. othonnaeflorus</u> DC.	AEN	
<u>S. oxyiriifolius</u> DC.	ATL	
<u>S. pyramidatus</u> DC.	TKL	endemic
<u>S. quinquelobus</u> (Thunb.) DC.	ATL	
<u>S. radicans</u> (L.f.) Sch. Bip.	KEN	
<u>S. ruwenzoriensis</u> S. Moore	CAL	
<u>S. sp.</u>		
<u>S. sp.</u>		
<u>S. sp.</u>		

<u>Sonchus asper</u> (L.) Hill	WID *
<u>Stoebe plumosa</u> Thunb.	CAL
<u>Tarchonanthus camphoratus</u> L.	TRW
<u>Ursinea anethoides</u> (DC.) N.E.Br.	CEN
<u>U. heterodonta</u> DC. (N.E.Br.)	CEN
<u>U. scariosa</u> (Ait.) Poir ssp. <u>scariosa</u>	CEN
<u>Vernonia capensis</u> (Houtt.) Druce	TRW

CONVOLVULACEAE

<u>Convolvulus bidentatus</u> Bernh. ap. Kraus.	CEN
<u>C. capensis</u> Burm. f.	CKL
<u>Falkia repens</u> L.f.	WID

CORNACEAE

<u>Curtisia dentata</u> (Burm. f). C.A. Sm.	AEN
---	-----

CRASSULACEAE

<u>Cotyledon orbiculata</u> L.	WID	endemic
<u>C. velutina</u> Hook.f.	TKL	
<u>Crassula capitella</u> ssp. <u>thyrsiflora</u> (Thunb.) Toelk.	KEN	
<u>C. ciliata</u> L.	CEN	
<u>C. cultrata</u> L.	TKL	
<u>C. ericoides</u> Haw.	CAL	
<u>C. expansa</u> Dryand ssp. <u>expansa</u>	WID	
<u>C. expansa</u> Dryand ssp. <u>filicaulis</u> (Haw.) Toelk.	CEN	
<u>C. mollis</u> Thunb.	KTL	
<u>C. muscosa</u> L.	KEN	
<u>C. nemorosa</u> (Eckl. & Zeyh.) Walp.	KEN	
<u>C. nudicaulis</u> L.	WID	
<u>C. orbicularis</u> L.	ATL	
<u>C. ovata</u> (Mill.) Druce	TKL	
<u>C. pellucida</u> L. ssp. <u>brachypetala</u> (Harv.) Toelk.	AEN	
<u>C. pellucida</u> L. ssp. <u>marginalis</u> (Dryand.) Toelk.	ATL	
<u>C. perforata</u> Thunb.	TKL	
<u>C. spathulata</u> Thunb.	AEN	
<u>C. subulata</u> L.	CEN	
<u>Kalanchoe rotundifolia</u> Haw.	WID	

CRUCIFERAE

<u>Heliophila brachycarpa</u> Meisn.	KEN
<u>H. linearis</u> (Thunb.) DC.	CKL
<u>H. suavissima</u> Burch. ex DC.	KEN
<u>H. subulata</u> Burch. ex DC.	CTL
<u>Lepidium africanum</u> (Burm.f.) DC.	WID
<u>L. ecklonii</u> Schrad.	WID
<u>Sisymbrium capense</u> Thunb.	KEN

CUCURBITACEAE

<u>Kedrostis nana</u> (Lam.) Cogn.	CTL
<u>Melothria cordata</u> (Thunb.) Cogn.	ATL

DIPSACEAE

<u>Cephalaria humilis</u> (Thunb.) R. & S.	CAL
<u>Scabiosa columbaria</u> L.	WID

DROSERACEAE

<u>Drosera aliciae</u> Hamet	CEN
<u>D. cistiflora</u> L.	CEN

EBENACEAE

<u>Diospyros dicrophylla</u> (Gand.) De Winter	TEN
<u>D. lyciodes</u> Desf.	TRW
<u>D. scabrida</u> (Harvey ex Hiern) De Winter	TEN
<u>D. villosa</u> (L.) De Winter	ATL
<u>Euclea crispa</u> (Thunb.) Sonder ex Gürke	TRW
<u>E. natalensis</u> A. DC.	TZL
<u>E. polyandra</u> E. Mey. ex Hiern	CEN
<u>E. racemosa</u> Murray	CTL
<u>E. schimperi</u> (A. DC.) Dandy	TZL
<u>E. undulata</u> Thunb.	KZL

ERICACEAE

<u>Coliostigma tenuifolium</u> Kl.	CEN	endemic
<u>C. zeyherianum</u> Kl.	CEN	endemic
<u>Erica cerinthoides</u> L.	CAL	
<u>E. chamissonis</u> Kl. ex Benth.	CEN	endemic
<u>E. chloroloma</u> Lindl.	CEN	endemic
<u>E. copiosa</u> Wendl.	CEN	
<u>E. decipiens</u> Spreng. f.	CEN	
<u>E. deliciosa</u> Wendl. f. ex Benth.	CEN	
<u>E. demissa</u> Kl. ex Benth.	CEN	endemic
<u>E. diaphana</u> Spreng.	CEN	
<u>E. floribunda</u> Lodd.	CEN	
<u>E. glandulosa</u> Th.	CEN	
<u>E. glumiflora</u> Kl. ex Benth.	CEN	endemic
<u>E. gracilis</u> Wendl.	CEN	
<u>E. harveiana</u> Guthr. & Bal.	CEN	endemic
<u>E. humansdorpensis</u> Compton	CEN	endemic
<u>E. maesta</u> Bol.	CAL	
<u>E. nemorosa</u> Kl. ex Benth.	CEN	
<u>E. pectinifolia</u> Salisb.	CEN	endemic
<u>E. sessiflora</u> L.f.	CEN	
<u>E. sparmannii</u> L.f.	CEN	endemic
<u>E. speciosa</u> Andr.	CEN	

<u>E. unilateralis</u> Kl.	CEN	endemic
<u>E. sp.</u>		
<u>E. sp.</u>		
<u>Scyphogyne</u> sp.		
<u>Simocheilus barbiger</u> Kl.	CEN	endemic
<u>Thamnus multiflorus</u> Kl.	CEN	endemic

EUPHORBIACEAE

<u>Adenocline actuta</u> (Thunb.) Baill.	AEN	
<u>A. pauciflorum</u> Turcz.	CEN	
<u>Clutia affinis</u> Sond.	CTL	
<u>C. africana</u> Poir.	CEN	
<u>C. alaternoides</u> L.	CEN	
<u>C. brevifolia</u> Sond.	CEN	
<u>C. daphnoides</u> Lam.	CTL	
<u>C. ericoides</u> Thunb.	CEN	
<u>C. polifolia</u> Jacq.	CEN	
<u>C. pulchella</u> L.	ATL	
<u>C. rubricaulis</u> Eckl. ex Sond.	CEN	
<u>Ctenomaria capensis</u> (Thunb.) Harv.	ATL	
<u>Euphorbia clava</u> Jacq.	TKL	endemic
<u>E. fimbriata</u> Scop.	TKL	endemic
<u>E. gorgonis</u> Berger	KEN	endemic
<u>E. grandidens</u> Haw.	TEN	
<u>E. kraussiana</u> Bernh.	AEN	
<u>E. mauritanica</u> L.	KEN	
<u>E. polygona</u> Haw.	CKL	endemic
<u>E. rhombifolia</u> Boiss.	TKL	
<u>E. silenifolia</u> (Haw.) Sweet	CEN	
<u>E. triangularis</u> Desf.	TEN	
<u>Lachnostylis hirta</u> (L.f.) Muell. Arg.	ATL	
<u>Leidesia obtusa</u> (Thunb.) Muell. Arg.	AEN	
<u>Phyllanthus heterophyllus</u> E. Mey. ex Muell. Arg.	CTL	
<u>P. incurvus</u> Thunb.	CKL	
<u>P. verrucosus</u> Thunb.	TEN	

FLACOURTIACEAE

<u>Dovyalis rhamnoides</u> (Burch. ex DC.) Burch. & Harvey	ATL	
<u>D. rotundifolia</u> (Thunb.) Thunb. & Harvey	TEN	
<u>Kiggelaria africana</u> L.	AEN	
<u>Scolopia mundii</u> (Eckl. & Zeyh.) Warb.	AEN	
<u>S. zeyheri</u> (Nees) Harvey	ATL	
<u>Trimeria grandifolia</u> (Hochst.) Warb. ssp. <u>grandifolia</u>	ATL	

GENTIANACEAE

<u>Chironia baccifera</u> L.	CTL	
<u>C. tetragona</u> L.f.	CEN	
<u>Sebaea aurea</u> (L.f.) Roem & Schult	CEN	
<u>S. sediodes</u> Gilg.	AEN	

GERANIACEAE

<u>Geranium incanum</u> Burm. f.	CAL	
<u>Monsonia emarginata</u> (L.f.) L'Herit	CAL	
<u>Pelargonium alchemilloides</u> (L.) L'Herit	WID	
<u>P. cafferum</u> Eckl. & Zeyh.	CAL	
<u>P. capitatum</u> (L.) Ait.	CTL	
<u>P. dichondraefolium</u> DC.	CAL	
<u>P. grossularioides</u> (L.) Ait.	CTL	
<u>P. hirsutum</u> Ait.	CEN	
<u>P. lobatum</u> (L.) Ait.	CEN	
<u>P. longifolium</u> Jacq.	CEN	
<u>P. odoratissimum</u> (L.) L'Herit	KEN	
<u>P. ovale</u> (Burm. f.) L'Herit ssp. <u>ovale</u>	CEN	
<u>P. ovale</u> (Burm. f.) L'Herit ssp. <u>veronicaefolium</u> (Eckl. & Zeyh.) Hugo	CEN	endemic
<u>P. peltatum</u> (L.) L'Herit	TKL	
<u>P. populifolium</u> Eckl. & Zeyh.	CEN	
<u>P. reniforme</u> Curtis	CAL	
<u>P. urbanum</u> Eckl. & Zeyh.	CEN	endemic

GESNERIACEAE

<u>Streptocarpus rexii</u> (Bowie) Lindl.	AEN	
---	-----	--

GUTTIFERAE

<u>Hypericum aethiopicum</u> Thunb. ssp. <u>aethiopicum</u>	CAL	
---	-----	--

HAMAMELIDACEAE

<u>Trichocladus ellipticus</u> Eckl. & Zeyh.	AEN	
--	-----	--

ICACINACEAE

<u>Apodytes dimidiata</u> E. Mey. ex Arn.	AEN	
---	-----	--

LABIATAE

<u>Leonotis leonotis</u> (L.) R.Br.	CAL	
<u>Plectranthus madagascariensis</u> (Pers.) Benth.	TEN	
<u>P. verticillaris</u> (L.f.) Druce	ATL	
<u>Salvia aurea</u> L.	CEN	
<u>S. triangularis</u> Thunb.	CKL	
<u>Stachys aethiopica</u> L.	WID	
<u>S. subsellis</u> Burch. ex Benth.	CTL	endemic
<u>Teucrium capense</u> Thunb.	WID	

LAURACEAE

<u>Cassytha ciliolata</u> Nees	CEN	
<u>Ocotea bullata</u> E. Mey. ex Meisn.	AEN	

LEGUMINOSAE

<u>Acacia karroo</u> Hayne	WID	
<u>Argyrolobium collinum</u> Eckl. & Zeyh.	CKL	
<u>A. crassifolium</u> Eckl. & Zeyh.	CKL	endemic
<u>A. incanum</u> Eckl. & Zeyh.	CEN	
<u>A. pumilum</u> Eckl. & Zeyh.	CKL	
<u>A. sericea</u>	CEN	endemic
<u>Aspalathus angustifolia</u> (Lam.) Dahlg. ssp. <u>angustifolia</u>	CEN	
<u>A. asparagoides</u> L.f. ssp. <u>rubro-fusca</u> (Eckl. & Zeyh.) Dahlg.	CEN	
<u>A. biflora</u> E. Mey. ssp. <u>longicarpa</u> R. Dahlgr.	CEN	
<u>A. cerrhantha</u> Eckl. & Zeyh.	CEN	
<u>A. chortophila</u> Eckl. & Zeyh. ssp. <u>chortophila</u>	CAL	
<u>A. chortophila</u> Eckl. & Zeyh. ssp. <u>kougaensis</u> R. Dahlgr.	CEN	
<u>A. collina</u> Eckl. & Zeyh. ssp. <u>collina</u>	CEN	
<u>A. hispida</u> Thunb. ssp. <u>albiflora</u> (Eckl. & Zeyh.) R. Dahlgr.	CEN	
<u>A. lactea</u> Thunb. ssp. <u>adelphea</u> (Eckl. & Zeyh.) R. Dahlgr.	CKL	
<u>A. nivea</u> Thunb.	CEN	endemic
<u>A. rubens</u> Thunb.	CEN	
<u>A. setacea</u> Eckl. & Zeyh.	CEN	endemic
<u>A. spinosa</u> L. ssp. <u>spinosa</u>	CAL	
<u>Cyclopia aurea</u> Fourc.	CEN	endemic
<u>C. subternata</u> Vog.	CEN	
<u>Dipogon lignosus</u> (L.) Verdc.	ATL	
<u>Dolichos hastaeformis</u> E. Mey.	TEN	
<u>Erythrina caffra</u> Thunb.	TEN	
<u>Indigofera candicans</u> Ait.	CEN	
<u>I. denudata</u> L.f.	CEN	
<u>I. glaucescens</u> Eckl. & Zeyh.	CEN	endemic
<u>I. heterophylla</u> Thunb.	CEN	
<u>I. heydantha</u> Eckl. & Zeyh.	AEN	
<u>I. hispida</u> Eckl. & Zeyh.	CEN	endemic
<u>I. incana</u> Thunb.	CEN	
<u>I. procumbens</u> L.	CEN	
<u>I. stenophylla</u> Eckl. & Zeyh.	CEN	endemic
<u>I. stricta</u> L.f.	CAL	
<u>I. sulcata</u> DC.	CEN	endemic
<u>I. zeyheri</u> Spreng.	CTL	
<u>I. sp.</u>		
<u>Lotononis pungens</u> Eckl. & Zeyh.	CKL	
<u>Medicago hispida</u> Gaertn.	WID *	
<u>Podalyria burchellii</u> DC.	CEN	
<u>P. myrtillifolia</u> (Retz.) Willd.	CEN	
<u>Priestleya hirsuta</u> (Thunb.) DC.	CEN	
<u>Psoralea bracteata</u> L.	CEN	
<u>P. decumbens</u> Ait.	CEN	
<u>P. cordata</u> (L.) Salter	CEN	
<u>P. laxa</u> Salter	CEN	
<u>P. pirinata</u> L.	CAL	
<u>P. polyphylla</u> Eckl. & Zeyh.	CEN	endemic
<u>P. repens</u> L.	CEN	
<u>P. rotundifolia</u> L.f.	CEN	

<u>P. tomentosa</u> Thunb.	CEN
<u>Rhynchosia capensis</u> (Burm.) Schinz	CEN
<u>R. caribaea</u> DC.	ATL
<u>R. pentheri</u> Schl. ex Zahlbr.	TEN
<u>R. totta</u> DC.	TRW
<u>Schotia afra</u> (L.) Thunb.	TKL
<u>S. latifolia</u> Jacq.	TEN
<u>Sutherlandia frutescens</u> (L.) R.Br.	CKL
<u>Tephrosia capensis</u> (Jacq.) Pers.	WID
<u>T. grandiflora</u> (Ait.) Pers.	CTL
<u>Trifolium burchellianum</u> Ser.	WID
<u>Vigna unguiculata</u> (L.) Walp.	ATL
<u>V. vexillata</u> (L.) A. Rich.	TEN

LINACEAE

<u>Linum africanum</u> L.	CEN
<u>L. thunbergii</u> Eckl. & Zeyh.	CAL

LOGANIACEAE

<u>Buddleja saligna</u> Willd.	WID
<u>Nuxia floribunda</u> Benth.	AEN

LORANTHACEAE

<u>Viscum capense</u> L.f.	WID
<u>V. obscurum</u> Thunb.	ATL
<u>V. rotundifolium</u> L.f.	TZL

MALVACEAE

<u>Abutilon sonneratianum</u> (L.) Sweet	TEN
<u>Hibiscus aethiopicus</u> L.	WID
<u>H. pusillus</u> Thunb.	WID
<u>H. trionum</u> L.	WID
<u>Sida ternata</u> L.f.	WID

MELIACEAE

<u>Ekebergia capensis</u> Sparrm.	AEN
-----------------------------------	-----

MENISPERMACEAE

<u>Antizoma capensis</u> (L.f.) Diels.	WID
--	-----

MONTINIACEAE

<u>Montinia caryophyllaceae</u> Thunb.	CKL
--	-----

MORACEAE

<u>Ficus burtt-davyi</u> Hutch.	TEN
---------------------------------	-----

MYRICACEAE

<u>Myrica cordifolia</u> L.	CTL	
<u>M. humilis</u> Cham. & Schlecht.	CEN	
<u>M. quercifolia</u> L.	CTL	
<u>M. serrata</u> Lam.	WID	

MYRSINACEAE

<u>Myrsine africana</u> L.	AEN	
<u>Rapanea gilliana</u> (Sonder.) Mez	CTL	endemic
<u>R. melanophloeos</u> (L.) Mez	AEN	

MYRTACEAE

<u>Eugenia capensis</u> (Eckl. & Zeyh.) Harvey & Sonder ssp. <u>zeyheri</u> (Harvey) F. White	TEN	
--	-----	--

OCHNACEAE

<u>Ochna arborea</u> Burch. ex DC.	ATL	
<u>O. serrulata</u> (Hochst.) Walp.	ATL	

OLEACEAE

<u>Jasminum angulare</u> Vahl	TEN	
<u>Linociera foveolata</u> (E. Meyer) Knobl.	ATL	
<u>Olea capensis</u> L. ssp. <u>capensis</u>	TRW	
<u>O. capensis</u> L. ssp. <u>macrocarpa</u> (C.H.Wright) Verdoorn	AEN	
<u>O. europaea</u>	WID	
<u>O. exasperata</u> Jacq.	CTL	
<u>Olinia ventosa</u> (L.) Cufod.	ATL	

OXALIDACEAE

<u>Oxalis algoensis</u> Eckl. & Zeyh.	CEN	
<u>O. ciliaris</u> Jacq.	CEN	
<u>O. imbricata</u> Eckl. & Zeyh.	CKL	
<u>O. incarnata</u> L.	CEN	
<u>O. obtusa</u> Eckl. & Zeyh.	CKL	
<u>O. polyphylla</u> Jacq.	CEN	
<u>O. psilopoda</u> Turcz	CEN	
<u>O. punctata</u> L.f.	CEN	
<u>O. purpurea</u> L.	CEN	
<u>O. smithiana</u> Eckl. & Zeyh.	CAL	
<u>O. stenorrhynca</u> Salter	ATL	endemic
<u>O. stellata</u> Eckl. & Zeyh.	CTL	
<u>O. sp.</u>		
<u>O. sp.</u>		

PENAEACEAE

<u>Penaea cneorum</u> Meerb. ssp. <u>ovata</u> Dahlgr.	CEN	
--	-----	--

PITTOSPORACEAE

<u>Pittosporum viridiflorum</u> Sims	AEN	
--------------------------------------	-----	--

PLUMBAGINACEAE

<u>Limonium scabrum</u> (Th.) O. Kze	CEN	
<u>Plumbago auriculata</u> Lam.	TZL	

POLYGALACEAE

<u>Muraltia alopecuroides</u> (L.) DC.	CEN	
<u>M. ciliaris</u> DC.	CEN	
<u>M. ericaefolia</u> DC.	CEN	
<u>M. juniperifolia</u> (Poir.) DC.	CEN	
<u>M. squarrosa</u> (L.f.) DC.	CEN	endemic
<u>M. sp.</u>		
<u>Nylandtia spinosa</u> (L.) Dumort	CEN	
<u>Polygala asbestina</u> Burch.	KEN	
<u>P. ericaefolia</u> Harv.	CEN	endemic
<u>P. fruticosa</u> Berg.	CAL	
<u>P. hamata</u> Burt-Davy.	TZL	
<u>P. microlopha</u> DC.	CEN	
<u>P. myrtifolia</u> L.	CTL	
<u>P. virgata</u> Thunb.	CAL	
<u>P. sp.</u>		

POLYGONACEAE

<u>Polygonum atraphaxoides</u> Thunb.	CEN	
<u>Rumex angiocarpus</u> Murb.	WID	*

PORTULACACEAE

<u>Portulacaria afra</u> Jacq.	TKL	
--------------------------------	-----	--

PROTEACEAE

<u>Leucadendron eucalyptifolium</u> Buek ex Meisn.	CEN	
<u>L. loerinse</u> Williams	CEN	endemic
<u>L. salignum</u> Berg.	CEN	
<u>Leucospermum cuneiforme</u> (Burm.f.) Rourke	CEN	
<u>Paranomus reflexus</u> (Phill. & Hutch.) N.E.Br.	CEN	endemic
<u>Protea cynaroides</u> (L.) L.	CEN	
<u>P. eximia</u> (Salisb. ex Knight) Fourc.	CEN	
<u>P. foliosa</u> Rourke	CEN	endemic
<u>P. mundii</u> Klotzch	CEN	
<u>P. neriifolia</u> R.Br.	CEN	
<u>P. nitida</u> Mill.	CEN	
<u>P. repens</u> (L.) L.	CEN	
<u>P. tenax</u> (Salisb.) R.Br.	CEN	endemic

PTAEROXYLACEAE

<u>Ptaeroxylon obliquum</u> (Thunb.) Radlk.	ATL	
---	-----	--

RANUNCULACEAE

<u>Clematis brachiata</u> Thunb.	ATL	
<u>Knowltonia capensis</u> (L.) Hutch.	CAL	

RHAMNACEAE

<u>Phyllica abietina</u> Eckl. & Zeyh.	CEN	endemic
<u>P. axillaris</u> Lam.	CEN	
<u>P. gnidioides</u> Eckl. & Zeyh.	CEN	endemic
<u>P. litoralis</u> D. Dietr.	CEN	endemic
<u>P. paniculata</u> Willd.	CAL	
<u>Rhamnus prinoides</u> L'Her.	AEN	
<u>Scutia myrtina</u> (Burm. f.) Kurz	ATL	

ROSACEAE

<u>Cliffortia burchellii</u> Stapf	CEN	
<u>C. drepanoides</u> Eckl. & Zeyh.	CEN	endemic
<u>C. ferruginea</u> L.f.	CEN	
<u>C. filicaulis</u> Schldl.	CEN	
<u>C. filifolia</u> L.f.	CEN	
<u>C. ilicifolia</u> L.	CEN	
<u>C. linearifolia</u> Eckl. & Zeyh.	CAL	
<u>C. stricta</u> H. Weim.	CEN	
<u>Rubus rigidus</u> Smith	AEN	

RUBIACEAE

<u>Anthospermum aethiopicum</u> L.	CAL	
<u>A. ciliare</u> L.	CEN	
<u>A. paniculatum</u> Cruse.	CEN	
<u>A. prostratum</u> (L.f.) Nees	CEN	
<u>Burchellia bubalina</u> (L.f.) Sims	ATL	
<u>Canthium ciliatum</u> (Klotzsch) Kuntze	ATL	
<u>C. inerme</u> (L.f.) Kuntze	ATL	
<u>C. mundianum</u> Cham. & Schlecht.	ATL	
<u>C. obovatum</u> Klotzsch	ATL	
<u>C. pauciflorum</u> (Klotzsch) Kuntze	AEN	
<u>C. spinosum</u> (Klotzsch) Kuntze	TEN	
<u>Carpacoce vaginellata</u> Salter	CEN	
<u>Rubia petiolaris</u> DC.	ATL	
<u>Xeromphis rudis</u> (E. Mey ex Harv.) Codd	ATL	

RUTACEAE

<u>Agathosma acutissima</u> Düm	CEN	endemic
<u>A. apiculata</u> G.F.W. Mey.	CEN	
<u>A. capensis</u> Düm	CEN	
<u>A. gonaquensis</u> Eckl. & Zeyh.	CEN	endemic
<u>A. hirta</u> Bartl. & Wendl.	CEN	endemic
<u>A. mundtii</u> Cham. & Schldl.	CEN	
<u>A. ovata</u> Pillans	CAL	
<u>A. pilifera</u> Schldl.	CEN	endemic
<u>A. puberula</u> Fourc.	CEN	endemic
<u>A. stenopetala</u> Steud.	CEN	endemic
<u>A. uncarpellata</u> Pillans	CEN	endemic
<u>A. venusta</u> Pillans	CEN	endemic
<u>Clausena anisata</u> (Willd.) Hook.f. ex Benth.	ATL	

<u>Diosma hirsuta</u> L.	CEN	
<u>D. prama</u> Williams	CEN	
<u>Vepris undulata</u> (Thunb.) Verdoorn & C.A. Smith	ATL	
<u>Zanthoxylum capense</u> (Thunb.) Harv.	ATL	

SALVADORACEAE

<u>Azima tetracantha</u> Lam.	TZL	
-------------------------------	-----	--

SANTALACEAE

<u>Colpoon compressum</u> Berg.	CTL	
<u>Rhoiacarpos capensis</u> (Harv.) A. DC.	TEN	endemic
<u>Thesidium exocarpaeoides</u> Sond.	CEN	
<u>Thesium capitatum</u> A.W. Hill	CEN	
<u>T. flexuosum</u> A.DC.	CKL	
<u>T. galioides</u> A.DC.	KEN	
<u>T. junceum</u> Bernh.	CEN	
<u>T. leptocaulis</u> Sond.	CEN	endemic
<u>T. nigromontanum</u> Sond.	CEN	
<u>T. quinqueflorum</u> Sond.	CEN	
<u>T. scandens</u> E. Mey.	CKL	endemic
<u>T. squarrosum</u> L.f.	CEN	
<u>T. strictum</u> Berg.	CEN	
<u>T. sp.</u>		
<u>T. sp.</u>		

SAPINDACEAE

<u>Allophylus decipiens</u> (Sond.) Radlk.	ATL	
<u>Dodonaea viscosa</u> Jacq.:	WID	
<u>Hippobromus pauciflorus</u> (L.f.) Radlk.	ATL	
<u>Pappea capensis</u> Eckl. & Zeyh.	TRW	
<u>Smellocphyllum capense</u> (Sond.) Radlk.	ATL	endemic

SAPOTACEAE

<u>Sideroxylon inerme</u> L.	TEN	
------------------------------	-----	--

SCROPHULARIACEAE

<u>Graderia scabra</u> (L.f.) Benth.	CAL	
<u>Halleria lucida</u> L.	AEN	
<u>Harveya capensis</u> Hook	CEN	
<u>H. purpurea</u> (L.f.) Harv.	CAL	
<u>Hyobanche sanguinea</u> L.	CEN	
<u>Manulea obovata</u> Benth.	CEN	
<u>Nemesia capensis</u> (Thunb.) O. Ktze	WID	
<u>Polycarena cuneifolia</u> (Benth.) Levyns	CEN	endemic
<u>Sutera aethiopica</u>	CEN	
<u>S. campanulata</u> (Benth.) O. Ktze	CAL	
<u>S. microphylla</u> (Benth.) Hiern.	CEN	
<u>S. pedunculata</u> (Andr.) Hiern.	CEN	
<u>S. pinnatifida</u> (Benth.) O. Ktze	KEN	

<u>S. polyantha</u> (Benth.) O. Ktze	WID	
<u>S. roseoflava</u> Hiern.	CTL	endemic
<u>Zaluzianskya capensis</u> Walp.	CAL	
<u>Z. maritima</u> (L.f.) Walp.	CAL	

SELAGINACEAE

<u>Hebenstreitia integrifolia</u> L.	WID	
<u>Selago canescens</u> L.f.	CEN	
<u>S. corymbosa</u> L.	CKL	
<u>S. dregei</u> Rolfe	CEN	
<u>S. glomerata</u> Thunb.	CEN	
<u>S. ramulosa</u> E. Mey.	CEN	
<u>Walafrida nitida</u> E. Mey.	CEN	
<u>W. sp.</u>		

SOLANACEAE

<u>Lycium afrum</u> L.	KEN	
<u>L. campanulatum</u> E. Mey.	KEN	
<u>Solanum coccineum</u> Jacq.	WID	
<u>S. quadrangulare</u> Thunb.	CTL	
<u>S. sodomaeum</u> Dunal	WID	

STERCULIACEAE

<u>Hermannia althaeoides</u> Link	CKL	
<u>H. filifolia</u> L.f.	KEN	
<u>H. flammea</u> Jacq.	CEN	
<u>H. hyssopifolia</u> L.	CEN	
<u>H. ovalis</u> Harv.	CKL	endemic
<u>H. salvifolia</u> L.f.	CEN	
<u>H. sulcata</u> Harv.	CKL	endemic
<u>H. velutina</u> DC.	CTL	
<u>Melhanian didyma</u> Eckl. & Zeyh.	ATL	

THYMELAEACEAE

<u>Gnidia anthylloides</u> (L.f.) Gilg.	CAL	
<u>G. coriaceae</u> Meisn.	CEN	endemic
<u>G. sericea</u> L.	CEN	
<u>G. setosa</u> Wickstr.	CEN	
<u>G. styphelioides</u> Meisn.	CEN	endemic
<u>Lachnaea burchellii</u> Meisn.	CEN	
<u>Passerina falcifolia</u> C.H. Wr.	CEN	endemic
<u>P. filiformis</u> L.	CTL	
<u>P. obtusifolia</u> Thoday	CEN	
<u>P. pendula</u> Eckl. & Zeyh.	CEN	endemic
<u>P. rigida</u> Wickstr.	CTL	
<u>P. rubra</u> C.H. Wr.	CEN	
<u>P. vulgaris</u> Thoday	CAL	
<u>Struthiola argentea</u> Lehm.	CEN	
<u>S. macowanii</u> C.H. Wr.	CEN	endemic
<u>S. parviflora</u> Bartl.	CEN	

TILIACEAE

Grewia occidentalis L.

ATL

UMBELLIFERAE

Alepidea capensis (Berg.) R.A. Dyer

CAL

Arctopus echinatus L.

CEN

Carum capense (Thunb.) Sond.

CKL

Centella coriacea Nannfd.

WID

C. eriantha (Rich.) Drude

CEN

C. glabrata L.

CTL

C. hermanniaefolia (Eckl. & Zeyh.) Domin

CEN

endemic

C. virgata L.

CEN

Heteromorpha arborescens (Spreng.) Cham. & Schlechtd.

TRW

Heteroptilis suffruticosus (Berg.) Leute

CEN

Lichtensteinia interrupta (Thunb.) E. Mey.

CTL

L. latifolia Eckl. & Zeyh.

CEN

Peucedanum capense (Thunb.) Sond

CEN

P. sp.Thunbergiella filifolius (Lam.) Wolff.

CEN

Torilis africana Spreng.

CEN

URTICACEAE

Urtica dioica L.

WID *

U. lobulata E. Mey.

WID

VERBENACEAE

Chascanum dehiscens (L.f.) Moldenke

TKL

VITACEAE

Rhoicissus digitata (L.f.) Gilg & Brandt

ATL

R. tomentosa (Lam.) Wild & R.B. Drumm.

ATL

R. tridentata (L.f.) Wild & R.B. Drumm.

TRW

ZYGOPHYLLACEAE

Zygophyllum morgsana L.

TKL

Z. uitenhaguense Sond.

TKL

endemic

¹ Endemic to either the Kaffrarian Transition Zone or the South Eastern Centre (see Paper 2).

* Introduced taxa.

Appendix Table 2.2. Kaffrarian Thicket community on Table Mountain sandstone, Humansdorp region

Community no.	1.1			1.2							
Relevé no.	170	171	175	142	169	172	143	144	146	204	145
Gonioma-Cassine sub-community											
Differential species											
Cassine reticulata	4	5	4								
Putterlickia pyracantha	5	3	3								
Euphorbia triangularis	5	2	4	1	2						
Euclea undulata		3	3								
Euryops euryopoides		3	1								
Cotyledon velutina	1	1	1	1							
Scadoxys puniceus	1	1	1								1
Gonioma-Maytenus sub-community											
Differential species											
Maytenus nemorosa				5	5	4	5	5	4	4	
Canthium inerme					3		3	3	3	4	1
Apodytes dimidiata				4	4			5	4	5	
Grewia occidentalis				1		2	3		2	3	
Asparagus macowanii				1			1	1	4	1	
Schoenoxiphium sparteum				1			3	5	3		
Sideroxylon inerme				5				1	1		5
Vepris undulata				2				3			3
Asparagus racemosus				2				1	1		
Senecio angulatus				1	1			1	1		
Podocarpus falcatus							4	1	5		1
Stipa dregeana							4	4		3	
Oxalis stenorrhyncha							1	1	1	1	4
Burchellia bubalina								3	4		2
Ctenomaria capensis								2	1	1	1
Dioscorea sylvatica								1	1	1	2
Cheilanthes bergiana							1				3
Pterocelastrus-Gonioma community											
General and infrequent species											
Pterocelastrus tricuspidatus	3	4	5	2	2	2	1	2	5	4	
Cassine aethiopica	4	3	1	4	3	2	4	4	3	3	
Dietes iridioides	4	3		2	5	5	5	5	5	5	3
Euclea racemosa ssp. macrophylla	2	2	3	2	1	1	3	1	3	3	3
Linociera foveolata	1	2		3	1	1	5	2	2	2	
Rhoicissus digitata	2	3		4		4	4	3	3	2	3
Carissa bispinosa	1	3	1	1	1	1	1	2	1	2	1
Panicum obumbratum	1	1		1	1	1	1	1	1	1	1
Gonioma kamassi	3	3	2		4	2			4		3
Cassine peragua	3	3	3	4	4	4	1	2	4		
Scutia myrtina	3	1		4	3	3	4		3	3	5
Diospyros dicrophylla	1		3	2	3		3	1	3	4	3
Aloe arborescens	3	3	2	1	2	2		1	4	3	
Asparagus setaceus	2	2		1	1		1	1	1	1	1
Rhoicarpus capensis	2	3	1	1				1	2	1	
Buddleja saligna	1		3	1			3	4	2	2	
Smellicium capense		5	2		1	1			3	4	
Lachnostylis hirta	4	4		3	4	4	2				
Maytenus acuminata	5		4	4	3	3		4			
Hippobromus pauciflorus	3			4	5	3	4				5
Hypoestes verticillaris		3	3					1	3	4	3
Allophylus decipiens	3		1				3	3		3	3
Asparagus aethiopicus	2	2	1		1	2				1	
Sarcostemma viminalis	1	2			3		3			1	
Cassine tetragona		2	1		1				2	2	
Dovyalis rhamnoides	1		3					1		1	1
Senecio deltoides	2	1					1			1	1
Olea europaea	2		2					3		3	
Plectranthus madagascariensis		3								3	3
Rhus longispina			1				1		3	2	
Rhus glauca			3		1			3			
Crassula pellucida			1			1				1	

Rare species:

Acokanthera oppositifolia (143:1), *Asplenium rutaefolium* (169:1), *Canthium ciliatum* (142:2), *C. pauciflorum* (144:2), *Capparis sepia* (143:2), *Clausena anisata* (204:2), *Crassula cultrata* (171:1), *C. orbicularis* (171:1), *C. spatulata* (146:2), *Ctenomaria capensis* (144:1), *Cussonia spicata* (171:3), *Delosperma ecklonis* (175:1), *Diospyros whyteana* (144:2), *Dryopteris inaequalis* (204:1), *Euryops spathaceus* (175:3), *Ficinia leiocarpa* (175:1), *Ficus burtt-davyi* (146:3), *Jasminum angulare* (142:2), *Kedrostis nana* (175:1), *Ledebouria* sp. (204:1), *Leidesia obtusa* (145:3), *Maytenus undata* (169:3), *Melothria cordata* (204:1), *Myrsine africana* (171:2), *Olea capensis* ssp. *capensis* (143:3), *Olinio cymosa* (146:4), *Ornithogalum* sp. (146:1), *Panicum deustum* (204:2), *Passerina filifolius* (171:1), *Pelargonium peltatum* (175:2), *Polygala myrtifolia* (204:2), *Rhus chirindensis* (143:1), *R. dentata* (146:2), *Schotia latifolia* (175:2), *Scolopia zeyheri* (143:2), *Senecio macroglossus* (145:2), *Thesium* sp. (175:1), *Trimeria grandifolia* ssp. *grandifolia* (143:2), *Tylophora cordata* (143:1), *Zanthoxylum capense* (143:1), *Zygophyllum morganii* (175:2).